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National Marine Fisheries Service
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A LINK BETWEEN SCIENCE AND MANAGEMENT IN FISHERIES

D. H. CUSHING[1]

ABSTRACT

In this paper a link is traced between science and management in that good conservation results from good science and that failure in management may be the result of scientific failure; but management failure is of course not the exclusive province of scientists. The argument is developed from a historical study of practice by fisheries scientists in the International Commissions.

The central problem of fisheries biology is to estimate the catch that can be safely taken from a stock. In Europe the problem was formulated by Petersen (1894) and Garstang (1900), who realized that if catches were too great they might subsequently decrease because the stock had been reduced too much. In the first decade of the present century exploratory voyages were made in the North Sea under the auspices of the International Council for the Exploration of the Sea (ICES). The high variability of the catches "precluded the possibility of any reliable combination of the trawling records" (Garstang, 1904). At the same time, Petersen said that overfishing was not the essential question and that the ICES should study the transplantation of small plaice as a method of conserving the weight of catch. Small plaice were caught in large numbers close to the continental coasts and, in summertime, the discards exceeded the retained catch by a factor of six. Petersen, Garstang, and Kyle (1907) subsequently wrote that "the plaice can be returned alive to the sea, where they . . . grow so much in size and value that the same fishermen who caught them in the first instance have a good chance of recapturing them when they have a greatly increased value." During their adult lives some demersal fish, such as plaice, grow by an order of magnitude or so, and if fished heavily the mean weight of the stock is reduced because the little fish do not have the chance to grow. The problem of growth overfishing as stated by Petersen is to conserve this loss of catch in weight.

The scientific judgment that catches were too variable led to a second judgment that management was impossible. The name of the "overfishing" committee in ICES was changed to that "investigating the biology of the Pleuronectidae and other trawl-caught fish." The solution recommended for the small plaice problem was to transplant them from the continental coasts to feeding grounds on or around the Dogger Bank. The ICES did not discuss the problem of overfishing again until after the first world war.

Management depends on the quality of scientific advice. Good science should lead to good management and failure in management is often due to scientific failure, although failure in management might be due to other causes. It has not been established yet whether the plaice stocks in the southern North Sea needed international management before the first world war, but the lack of management was not based on such a judgment; it was because the scientists could not assess the variability of catches, which was not surprising at that time because statistical techniques were not very well developed. This paper traces similar links between science and management in the subsequent history of fisheries science; the historical information is taken from a study of the development of the fisheries commissions in Cushing (1972).

THE DESCRIPTIVE MODEL

During the thirties, changes in populations were accounted for in the theory of balance; for example, a decrement in stock is compensated by an increment in recruitment per unit stock, and as fishing mortality increases a relative increase in recruitment is to be expected. Thompson and Bell (1934) and Graham (1935) stated explicitly that recruitment would not be reduced in magnitude by fishing at the stock levels normally exploited; they both worked on flatfish and their conclusion was well fitted to flatfish biology, if not to clupeids

[1]Ministry of Agriculture, Fisheries and Food, Fisheries Laboratory, Lowestoft, Suffolk, UK.

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or gadoids. Both plaice and halibut grow by more than an order of magnitude during their adult lives. Cushing (1972) distinguished growth overfishing from recruitment overfishing. In the first the stock loses weight by too much fishing, as Petersen suggested, but recruitment is not affected. In the second, recruitment is affected; it is noticeable in the pelagic stocks at a lower rate of exploitation than in the demersal stocks because the pelagic fishes have less capacity for stabilization, being less fecund.

Populations were well described by the logistic curve, which expressed the theory of balance in stating that any change in the carrying capacity of the environment was compensated by a change in the net rate of increase of the stock. From the changes in biomass in time, average estimates of the two parameters (net rate of increase and carrying capacity) can be obtained. Such models are called descriptive because the parameters are not estimated independently but are derived from the changes in biomass. In fish populations the contributions of growth and recruitment are compounded in the application of the logistic curve, whereas it would be desirable to distinguish them. Both Thompson and Bell (1934) and Graham (1935) concluded from the application of the logistic curve that age determination was no longer necessary. Had this conclusion been applied quite firmly the distinction between the effects of growth and recruitment in fish populations would have become impossible.

Graham's (1935) major explicit achievement was the application of the logistic curve to fish populations. Another achievement, an implicit one, was to encourage the application of the methods of operational research arising from the second world war to fish population dynamics by Beverton and Holt (1957), which led to the solution of the problem of growth overfishing. The logistic curve was developed more fully by Schaefer (1954, 1957). He derived a catchability coefficient from the relation of stock density to fishing effort and used it to obtain catch, which he then related to effort in the form of a parabola. Over a long time period, enough annual observations give an estimate of maximum sustainable yield. The advantage of this method is that the result can be expressed simply and convincingly. The disadvantages are 1) that at least a patient decade of data collection is needed to establish the position of the maximum, given a sufficient spread of fishing effort and 2) that upward or downward trends in recruitment would be distinguished with difficulty.

THE ANALYTIC MODEL

The first analytic model was Russell's (1931) in which the changes in stock were separated into components of growth, recruitment, and mortality. Beverton and Holt (1957) devised a series of models, including the well-known yield per recruit one and the less well-known self-regenerating yield curve, in which they incorporated their stock and recruitment relationships. The catch, or yield, was expressed as a function of fishing mortality and of the age at first capture. The most important point about the yield per recruit model is that the maximum yield is obtained from information on growth and fishing mortality, independently of the catches. There is no need to wait for a long time to establish the curve, and management decisions can be taken quickly, other considerations being equal.

The yield per recruit model was the theoretical solution to the problem of growth overfishing, and the practical solution was to increase the age at first capture with increased mesh size in the trawls. For management it is a clear solution and it is likely that the present agreement on management in the North Atlantic originated in its simplicity. There were lengthy discussions on the science and on the technology, but there are now agreed minimum landed sizes and minimum mesh sizes for a number of species throughout the North Atlantic. It must be said, however, that conservation by mesh regulation is least conservation because it is adapted to the smaller and numerous species like the haddock in the North Sea; larger species (for example, cod or turbot) are not necessarily conserved there as well as they might be.

In the yield per recruit model it is assumed that recruitment does not decline under the pressure of fishing. The argument presented by Beverton and Holt was that recruitment is so variable that the downward trend at low stock would be very difficult to detect. In management there was an unforeseen consequence: that fishing could continue until recruitment was seen to fail. Then, because of the same high variability of recruitment, fishing would continue until it was too late. However, with care, the yield per recruit model can be used when the stock and recruitment relationship is unknown; for example, if fishing is reduced, the yield per recruit will not decline and

may even rise if recruitment rises with reduced fishing.

It is likely that if fishing mortality is restrained to the maximum of the yield per recruit curves of most demersal fishes, recruitment would not be very much impaired. However, the curve for the herring is asymptotic and it was tacitly believed that the herring could be fished very hard merely because of the shape of the yield per recruit curve. Another consequence was that the maximum for the cod in the Barents Sea was overshot because in international terms a high catch was needed at the cost of a decreased catch per effort. The recruitment to the Barents Sea stock was severely reduced.

The collapse of herring fisheries throughout the northeast Atlantic and the failure of recruitment to the Arcto-Norwegian cod stock have been attributed to failure in the Commissions. These Commissions, however, are only as good as their scientific advice, and the two great failures are attributable to the unstated concept that fishing could continue until recruitment was seen to fail. Then failure had to be attributed either to natural causes or to fishing, and stocks collapsed while the scientists disputed the two possibilities. If recruitment overfishing had been recognized as a problem, perhaps collapse might have been avoided. The solution to the problem of growth overfishing inadvertently generated the problem of recruitment overfishing.

STOCK AND RECRUITMENT

The dependence of recruitment on parent stock was formulated by Ricker (1954, 1958), but the variability of recruitment is very high and the curve can only be fitted when decades of annual data have been collected. Any decision on how much fishing should be allowed is perhaps delayed for statistical reasons and management cannot proceed. On the other hand, if recruitment were considered to be independent of parent stock, management could start to take decisions more quickly. With hindsight, the assumption made by Thompson and Bell (1934) and Graham (1935) can be justified because their work formed the scientific basis of all international conservation in the North Atlantic and North Pacific. However, the danger of such a procedure is that any decline in recruitment tends to be attributed to natural causes rather than to fishing, and this step has sometimes been taken without evidence.

It is in the nature of the stock and recruitment problem that there should be confusion about attributing decline in recruitment to natural or to man-made causes. However, Cushing and Harris (1973) have devised a method of fitting the Ricker curve which sets confidence limits to the position of the curve itself; the standard deviation of residuals sets limits to the variation of recruitment. Then if stock is near that value which generates maximum recruitment per unit stock, any recruitment that falls below the standard deviation of the residuals has failed through natural causes. If stock is low, such a distinction cannot be made (because any recruitment below the standard deviation of the residuals is zero) and failure is attributed to natural or to man-made causes without evidence either way; however, a prudent manager might prefer to assume that recruitment declined under the pressure of fishing and to take appropriate action in the hope that the stock would recover, as recently happened with the British Columbia herring stock.

The stocks that have failed because of this dilemma are the California sardine, the Japanese sardine, and the northeast Atlantic herring; the Arcto-Norwegian cod stock might fail for the same reason. The failures of the first three were attributed to environmental factors on evidence that is only circumstantial; more recent evidence suggests that failure might have been due to fishing. To pursue the argument further is sterile. The scientific failure was the inability to make clear the distinction between natural and man-made causes. The failure in management was to delay action until the distinction could be made, whereas a prudent manager should have feared the effect of fishing upon recruitment.

In the stock and recruitment problem, long data series are needed before any management decision can be taken. When the development of a fishery proceeded slowly, this may not have mattered because the maximum yield was attained by gentle increments. Today, however, stocks are exploited rapidly, and there is the possibility that recruitment will be diminished before the data are available to describe the maximum sustained yield. What is needed is an analytic model of the stock and recruitment relationship on the lines of that of the yield per recruit one, on the basis of which decisions on management can be made quickly without the laborious acquisition of long series of data.

There are two large fisheries in the Pacific, on the Peruvian anchoveta and on the Alaska pollack. Recently the anchoveta recruitment failed, possibly due to fishing and possibly due to El Niño and perhaps due to both; because there is only about one decade of observations, the cause of failure will probably remain unknown, although it must always be admitted that the fishing mortality is high. In the Bering Sea there is a rising fishery on the Alaska pollack that also had been in existence for less than a decade. The potential managers of this fishery might like to have available now a yield curve before the data are available to describe the stock and recruitment curve. The source of scientific failure here is the inability to generate an analytic stock and recruitment model.

SCIENCE AND MANAGEMENT IN THE COMMISSIONS

When a fish stock fails the question arises whether the failure should be attributed to the Commission charged with its management or to the scientists. There is a distinction between the North Atlantic Commissions and those in the North Pacific. In the North Atlantic the two institutions (International Commission for the Northwest Atlantic Fisheries and Northeast Atlantic Fisheries Commission) are responsible for all stocks exploited in the area, whereas in the eastern North Pacific only those of interest to North American fishermen are conserved. Consequently the Commissions in the North Atlantic cannot disclaim responsibility for any failures that occur in their area, whereas the North Pacific Commissions may be able to do so.

In the North Atlantic, decline of the main demersal stocks has with one exception been prevented. The best conservation has not yet been achieved, but with the use of catch quotas and international enforcement there is considerable hope that conservation will ultimately be very effective. The scientific basis for this was the initial use of the yield per recruit model and in recent years the successful application of first, cohort analysis (Gulland, 1967), and secondly, the Clayden model (Clayden, 1972). On the other hand, the collapse of herring stocks in the northeast Atlantic was due entirely to the scientific failure to understand the nature of the stock and recruitment problem. Both success and failure in the Commissions can be linked to success or failure in the science.

In the North Pacific there are large areas of unregulated fishery, which the North Pacific Commission has not taken under its aegis. The cause of the increase in the maximum sustainable yield of the yellowfin tuna in the area of the Inter-American Tropical Tuna Commission is unknown, although a number of possible reasons have been cited. Halibut are caught by trawl by nations outside the control of the International Pacific Halibut Commission. The question of the offshore exploitation of the Pacific salmon stocks remains unresolved because the boundary between the North American and Asian stocks is not precise and the degree of mixture in the exploited area has not been established.

It remains true, of course, that the stock density of the halibut recovered from 1930 to 1960 by the action of the Halibut Commission, that the offshore exploitation of the North American salmon was prevented by the abstention principle, and that the yellowfin tuna stock is well exploited. Some of the failures in the North Pacific, like those in the North Atlantic, are rooted in scientific deficiencies (apart from the North Pacific failure to consider stocks that are outside the aegis of the Commissions).

The International Whaling Commission failed to conserve the stock of blue whales. The problem was solved in principle for the fin whale by Ruud (International Whaling Commission, 1956) but the solution was rejected by Schlijper (International Whaling Commission, 1957) who said that the age determination was faulty. The Committee of Four evaded this by expressing the results in the form of a Schaefer curve (International Whaling Commission, 1964); Schlijper never saw that age determination was used in the estimation of (recruitment less mortality) which played a considerable part in the solution. Part of the failure to conserve the stock was the delay in reaching an agreed scientific solution.

In contrast to the Whaling Commission, the North Pacific Fur Seal Commission has been well served by its scientists. A form of stock and recruitment relation has been established and the surplus stock is taken each year at somewhere near the best point for exploitation, and some progress has been made towards establishing the nature of the density-dependent control in the population. The Fur Seal Commission is the oldest of the international commissions and its records go back a long way, into the early 19th century.

From this very brief account of the role of

fisheries science in the Commissions there is one general conclusion, that when the science is successful the Commissions can work well but when the scientific evidence is confused the Commissions may fail. Of course, failure may occur for other reasons; for example, a proposal in the ICES to close the small plaice grounds in 1923 was rejected by the British fishing industry in 1926.

THE NATURE OF FISHERIES SCIENCE

The organization of knowledge into science is based on the establishment of laws that interlock. Each law subsumes much information and the network of laws comprises the body of the science. Advance in science is made by the addition to or the rearrangement of the network. Any scientific conclusion is judged in relation to the general framework, and it is tested in the premises and extensions of the argument in the network. It is sometimes said that the end of a scientific procedure is to establish a correlation; without denying the use of correlation, the most important point is to establish whether the correlation is likely and how it fits into the general scientific framework.

In a highly developed science such judgments are made frequently, but in a more primitive one like fisheries biology the necessary network has not yet been established. For example, all our information on stocks depends on catches, with the various biases in availability included; independent methods of estimating stock are being developed but they are not yet reliable. In a highly developed science, a number of methods independently yield the same result; fisheries biologists are pleased to estimate fishing mortality but very rarely is more than one method used. Natural mortality is estimated as the difference between total mortality and fishing mortality, and there is very little independent evidence of its magnitude. The information needed is accumulating quite quickly but the science remains a little weak.

Because biological material is highly variable, any biologist needs a working knowledge of statistics. Without denigrating this very real need, the science needs more than statistics, more information, more hypotheses, and more insight. It has sometimes been stated that fish stocks could be assessed by the study of ecosystems rather than by the study of single populations. This is rubbish; it is my view that not enough is known of any one population primarily because we have examined adult animals to the exclusion of the juveniles. I do not mean that we know nothing of fish larvae or 0-group fish, but that we know too little of their growth rates and death rates. With more knowledge of this sort, the problems of the regulation of numbers and of competition might be solved and we might at the same time learn something of how an ecosystem itself is regulated.

It has been said that fisheries science is fully developed and that its techniques are quite reliable. Much is known about the Pacific salmon but it is only a small fraction of what is needed. It has been said that stock and recruitment is the last problem in fish population dynamics. It is the study of the regulation of numbers, of competition between species, and of the variability of recruitment. In other words, it is the central problem of population dynamics. There is a sense in which fisheries biologists have passed through a long apprenticeship before they have embarked on the real problem that concerns them.

CONCLUSION

The international management of fisheries has developed slowly since it started during the second and third decades of the present century. There are many reasons for this, economic, social, and political; indeed the agreement achieved between nations is considerable when one considers all the difficulties involved. One of the reasons for this slow development, but not the only one, is that where the science has failed, so has management. Conversely, where the science has been successful, management can proceed with confidence, other things being equal. One would expect a link to exist between science and management, as it does in other fields.

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DEVELOPMENT AND DISTRIBUTION OF LARVAE AND JUVENILES OF *SEBASTOLOBUS* (PISCES; FAMILY SCORPAENIDAE)

H. GEOFFREY MOSER[1]

ABSTRACT

The North Pacific scorpaenid genus *Sebastolobus* is composed of three deepwater coastal species of potential commercial importance. They are oviparous and produce bilobed gelatinous egg masses that float to the surface waters where hatching and larval development occur. Transformation into pelagic juveniles occurs at about 20 mm length. The pelagic stage of *S. alascanus* is relatively short-lived, as they transform into benthic juveniles at 22 to 27 mm length. In the deep-living *S. altivelis* the juveniles remain pelagic for well over a year and grow as large as 56 mm.

Larvae of the two species mentioned are collected regularly on plankton surveys of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and pelagic and benthic juveniles are common constituents of mid-water and bottom trawls taken in the CalCOFI region. In this paper specimens from these sources are used to describe the larval and juvenile stages of the two species and to show the striking morphological changes which occur during development. Also presented are data on geographic distribution and patterns of seasonal abundance of larvae. Larvae of *Sebastolobus* smaller than 10.0 mm could not be distinguished to species.

Knowledge of the life history of the scorpionfish genus *Sebastolobus* is scanty. Pearcy (1962) described the floating egg masses, the developing embryos, and the newly hatched larvae of *Sebastolobus*. The larvae of *Sebastolobus* occur in the plankton collections of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and can be differentiated from those of *Sebastes* on the basis of the spination of the parietal ridge (Ahlstrom, 1961). Information on the distribution and abundance of *Sebastolobus* larvae in CalCOFI has hitherto not appeared in the literature, nor has a description of the larval stages. It is the purpose of this paper to fill that void and also to describe the distinctive juvenile stages of *S. altivelis* and *S. alascanus*, which are common constituents of mid-water trawl catches in the eastern North Pacific.

The three known species of *Sebastolobus* inhabit the coastal waters of the North Pacific. *Sebastolobus altivelis* ranges from the southern tip of Baja California to the Aleutian Islands while *S. alascanus* is found from northern Baja California to the Bering Sea and the Commander Islands off the Asiatic mainland. The Asian species, *S. macrochir*, ranges from the coast of Japan northward to the Bering Sea south of Cape Navarin and into the Sea of Okhotsk (Barsukov, 1964). At present the commercial catch of *Sebastolobus* is small, however, data of Best (1964) and Alverson, Pruter, and Ronholt (1964) suggest that these fishes may constitute a substantial resource in the deep coastal waters of the northeast Pacific.

The taxonomic characters of the adult members of this genus have been reviewed by a number of investigators (Starks, 1898; Hubbs, 1926; Matsubara, 1943; Phillips, 1957; Barsukov, 1964; Miller and Lea, 1972). *Sebastolobus* is distinguished from other scorpaenid genera by the unusual pectoral fins, each of which is separated by a notch into dorsal and ventral lobes, by possessing more vertebrae (28 to 31) and dorsal spines (15 to 17), a complete set of circumorbital bones, an uppermost pectoral radial which is free from the scapula, and by a suborbital stay with a broad posterior end anchored firmly onto the preopercular bone. The two North American species may be separated on the basis of the shape and number of rays in the spinous dorsal fin. In *S. altivelis* the third spine is the longest while in *S. alascanus* the fourth or fifth spine is the longest. The former species usually has 15 (rarely 16) spinous dorsal rays while the latter has 16 or 17 (rarely 15) rays. Also, *S. altivelis* usually has 29 (rarely 28) vertebrae and *S. alascanus* has 30 (rarely 31). The Asian species, *S.*

[1]Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92037.

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macrochir, is deeper bodied than the North American species and has a relatively narrower caudal peduncle. Counts of its spinous dorsal rays and vertebrae are close to those of *S. altivelis*.

Hubbs (1926), Barsukov (1964), and Miller and Lea (1972) have given information on the bathymetric ranges of the adults. In summary, *S. altivelis* occurs typically at 550 to 1,300 m with known depth extremes of 200 to 1,550 m. Everywhere along its latitudinal range *S. altivelis* is deeper living than *S. alascanus*, although there is some overlap and the two species are occasionally taken in the same trawls. *Sebastolobus alascanus* commonly occurs at 180 to 440 m, with known depth extremes of 18 to 1,524 m. *Sebastolobus macrochir* occurs commonly at 400 to 640 m.

MATERIALS AND METHODS

Larvae of *Sebastolobus* from 2 yr (1960, 1966) of CalCOFI survey cruises were identified and counted. From these a developmental series that encompassed the entire larval period was established. Larvae of this series were measured with the ocular micrometer of a stereoscopic microscope, according to the methods of Moser (1967, 1972), to produce the tables of morphometrics (Tables 1-3) needed for comparison of body proportions of *S. altivelis* and *S. alascanus*. This series also provided the specimens needed to describe the general morphology and melanophore pattern of the larvae. Measurements of four pelagic juveniles of *S. macrochir* are given in Table 4. An abbreviated series of *S. altivelis* and *S. alascanus* was selected, cleared with a graded series of KOH-glycerin solutions and stained with Alizarin Red-S to produce tables of meristics (Tables 5, 6).

The pelagic juvenile stages of the two species were obtained from the mid-water trawl collections of the Los Angeles County Museum of Natural History (LACM), the Scripps Institution of Oceanography (SIO), and the Southwest Fisheries Center. Demersal juveniles were obtained from otter trawl collections of LACM and SIO. As for larvae, series of juveniles were established for analysis of morphometrics (Tables 2-4), pigment pattern, and meristic characters (Tables 5, 6). In this paper the term "body length" refers to the distance from the snout to the tip of the notochord in larvae which have not yet formed the caudal fin. After dorsad flexion of the tip of the notochord and completion of caudal fin formation "body length" refers to standard length (distance from snout to posterior edge of hypural plate).

TABLE 1.—Measurements (mm) of *Sebastolobus* spp. larvae. Specimens between dashed lines are undergoing notochord flexion.

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-dorsal fin	Snout-anal fin
3.0	1.3	0.50	0.08	0.20	0.60	0.3	0.14			
3.5	1.4	0.80	0.18	0.25	0.52	0.23	0.20			
3.8	1.6	1.0	0.22	0.27	0.68	0.40	0.38			
4.2	1.8	1.2	0.25	0.30	0.86	0.45	0.40			
4.7	1.9	1.2	0.31	0.30	0.80	0.46	-			
5.0	2.0	1.4	0.35	0.33	0.90	0.65	0.50			
5.2	2.1	1.4	0.43	0.40	1.0	0.62	0.55			
5.5	2.3	1.6	0.42	0.35	1.1	0.65	0.58			
5.7	2.3	1.7	0.56	0.40	1.2	0.95	0.85			
5.8	2.4	1.7	0.51	0.39	1.2	1.0	0.78			
5.9	2.6	1.8	0.62	0.47	1.6	1.0	0.75			
6.0	2.7	1.8	0.55	0.51	1.8	1.3	0.85	0.22	2.3	3.4
6.2	2.7	1.9	0.70	0.48	1.6	1.4	0.90	0.20	-	-
6.4	2.7	1.8	0.60	0.45	1.5	1.2	0.85	0.13	-	-
6.7	3.1	1.9	0.82	0.55	1.8	1.4	1.0	0.15	3.9	3.9
6.8	2.8	2.0	0.82	0.52	1.8	1.4	1.1	0.17	-	3.2
6.9	3.3	2.2	0.80	0.58	2.0	1.5	1.2	0.25	2.7	4.1
7.1	3.5	2.5	0.82	0.71	2.4	1.8	1.2	0.80	2.5	4.2
7.3	3.8	2.5	0.95	0.76	2.4	1.8	1.4	0.85	2.7	4.4
7.7	4.2	2.7	1.1	0.75	2.8	2.1	1.5	0.85	2.9	4.5
7.8	4.3	3.1	1.1	0.82	2.6	2.1	1.4	1.2	3.2	4.8
8.3	4.4	3.1	1.1	0.79	2.6	2.0	1.4	1.0	3.1	4.9
8.6	4.8	3.2	1.2	0.92	3.1	2.4	1.7	1.4	3.5	5.3
8.9	5.2	3.3	1.2	1.0	3.1	2.5	1.7	1.4	3.8	5.4
9.2	5.2	3.5	1.2	1.0	3.2	2.7	1.5	1.5	3.8	5.6
9.6	5.4	3.5	1.2	1.1	3.7	2.8	1.8	1.7	4.1	5.8

TABLE 2.—Measurements (mm) of *Sebastolobus altivelis*. Specimens below dashed line have completed transformation into pelagic juvenile stage.

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-dorsal fin	Snout-anal fin
10.1	6.2	3.8	1.2	1.2	3.8	2.8	1.8	1.7	4.2	6.4
10.5	6.5	4.2	-	1.2	3.9	3.0	1.9	1.8	4.4	6.7
11.2	6.9	4.5	1.3	1.4	4.2	3.5	2.1	2.4	5.2	7.3
12.7	7.3	4.6	1.3	1.5	4.7	3.8	2.0	2.5	5.4	7.9
13.4	8.0	5.0	1.5	1.6	4.8	3.7	2.0	2.5	5.4	8.3
14.4	8.8	6.2	1.7	2.1	5.7	5.0	2.7	3.1	6.0	9.6
15.2	10.1	6.1	1.8	1.9	6.3	5.2	2.8	2.9	6.7	10.6
15.4	9.8	6.0	1.7	2.2	6.4	4.7	2.8	2.9	6.9	10.1
15.4	9.9	6.5	1.9	2.2	6.3	5.8	2.9	3.8	6.8	11.0
15.7	10.3	6.8	2.1	2.1	6.9	5.8	2.9	3.8	6.7	10.8
16.0	10.3	6.2	1.8	2.0	7.1	5.4	3.1	3.3	7.0	10.6
16.3	10.3	7.2	2.1	2.2	6.6	6.2	3.0	4.0	6.8	11.2
16.6	10.8	7.4	1.8	2.4	6.6	6.4	3.0	3.4	7.6	11.8
16.7	11.2	6.7	1.9	2.2	7.5	5.8	3.2	3.3	7.1	11.3
17.6	11.5	7.6	2.0	2.5	7.2	6.8	3.2	4.2	7.1	12.2
17.6	11.7	7.0	1.9	2.4	7.3	5.9	3.1	3.8	7.7	12.0
18.2	12.0	7.7	2.1	2.6	7.3	6.3	3.1	4.2	7.8	12.7
18.4	12.5	7.1	2.0	2.5	8.3	6.2	3.6	4.2	7.5	12.8
19.3	13.2	7.9	2.1	2.5	8.5	6.7	3.8	3.8	8.3	13.4
19.4	13.0	8.5	2.3	2.5	8.7	7.6	3.8	4.7	8.4	14.0
20.7	13.8	8.5	2.6	2.3	8.4	7.6	3.7	4.8	8.6	14.7
21.3	14.9	9.2	2.8	2.8	9.0	8.1	3.8	4.8	9.5	15.2
22.6	15.9	9.6	2.5	3.1	9.2	8.8	4.2	5.6	9.5	16.7
23.4	16.6	9.8	2.5	2.7	10.1	9.0	4.4	5.6	9.5	17.4
24.5	17.7	10.8	2.9	3.4	11.0	10.0	4.5	5.8	10.1	18.1
25.8	18.6	10.6	2.9	2.9	11.3	9.3	4.4	5.9	10.1	18.9
26.8	17.7	10.6	2.8	3.8	10.6	11.0	4.8	6.5	10.1	18.8
27.7	20.3	11.5	2.9	3.6	12.2	11.0	5.4	7.1	11.7	22.0
28.3	20.3	12.0	3.2	3.7	12.2	11.5	5.0	7.1	11.5	21.8
29.4	20.4	12.3	3.3	3.8	11.5	11.5	5.2	7.2	12.3	21.1
30.5	21.1	13.0	3.8	3.6	11.7	11.7	5.4	7.6	12.3	23.0
31.4	21.1	12.3	3.2	3.5	13.7	12.2	5.8	7.5	12.3	22.9
32.4	21.1	12.5	3.5	3.6	13.0	12.8	5.8	8.3	12.5	22.2
33.6	23.1	14.0	4.2	4.2	13.5	11.7	5.8	7.5	12.8	25.1
34.6	23.5	13.4	3.8	3.8	14.2	13.5	6.0	8.2	13.7	25.5
36.5	25.0	15.2	4.2	4.8	15.5	14.7	6.7	9.2	14.9	27.5
37.5	25.8	15.0	4.2	4.6	15.9	14.4	6.7	8.3	14.7	27.6
38.5	25.6	15.2	4.0	4.8	16.0	15.7	6.6	9.8	15.2	27.5
39.5	27.9	16.2	5.0	4.8	16.0	15.0	6.7	8.9	16.0	29.9
40.4	27.1	16.4	5.0	4.8	15.2	15.0	6.8	10.8	16.0	30.0
41.6	27.9	16.4	4.3	5.8	15.9	15.2	7.1	10.1	16.2	29.6
42.3	28.1	16.9	4.6	5.2	17.4	15.2	7.2	10.0	15.9	29.4
43.5	30.1	16.9	5.2	5.4	16.0	14.7	6.7	9.5	17.4	32.4
44.4	30.0	17.9	-	4.8	16.4	16.4	7.1	9.5	17.2	32.2
45.1	29.5	18.2	4.8	5.4	17.6	16.0	7.8	10.1	17.2	32.0
46.2	30.7	17.9	5.0	4.9	17.7	17.1	8.1	11.5	17.1	33.5
47.1	30.2	18.1	5.0	5.6	17.1	15.2	7.0	10.3	17.7	33.0
48.5	32.0	18.6	5.4	5.8	18.6	16.9	7.8	10.5	17.7	34.7
49.5	32.2	19.8	5.0	5.8	18.6	18.1	8.3	11.8	16.4	36.2
51.3	37.0	20.6	6.7	5.8	18.8	17.4	8.0	11.3	18.9	40.0
53.5	35.7	20.6	6.2	7.5	18.6	16.9	8.2	11.0	18.7	37.8
56.0	37.6	21.4	5.8	7.7	19.2	19.8	8.3	12.3	20.3	40.6
*42.0	26.8	16.6	4.6	5.6	12.0	12.7	6.0	9.3	16.4	29.0
*47.4	29.6	17.7	4.7	6.9	13.9	13.5	6.8	10.1	18.1	31.7
*48.1	31.4	19.1	5.2	7.3	14.4	15.2	7.0	11.5	17.9	33.5
*50.3	33.0	19.2	5.4	7.3	14.0	13.8	7.1	11.8	18.8	35.3
*51.0	33.0	19.5	4.7	7.2	15.0	16.2	7.5	11.2	18.7	35.2
*53.0	33.4	20.5	5.4	8.6	14.6	15.5	7.0	12.1	19.9	37.7
*54.0	35.4	19.7	5.9	7.3	15.5	17.7	7.8	12.6	20.6	38.4
*56.0	35.2	21.1	5.6	7.7	15.5	16.4	7.4	12.6	20.8	38.1
*57.5	37.2	21.4	5.6	8.0	15.3	16.7	8.1	12.5	21.1	40.3
*58.6	37.9	22.6	6.0	8.7	16.5	16.9	8.2	12.7	21.6	40.6
*60.0	38.0	22.0	6.0	8.4	16.2	15.1	8.1	12.8	21.5	41.6

*Benthic juvenile.

TABLE 3.—Measurements (mm) of larvae and juveniles of *Sebastolobus alascanus*.

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-dorsal fin	Snout anal fin
10.3	6.2	4.2	1.5	1.2	4.0	3.2	1.6	1.9	4.3	6.8
11.2	7.4	5.0	1.8	1.3	4.1	3.2	1.7	2.1	5.0	7.7
11.7	7.2	5.0	-	1.3	3.9	3.1	1.8	2.1	5.1	7.7
12.5	7.7	4.7	1.7	1.5	4.5	3.6	1.8	2.4	5.4	8.3
13.2	7.3	5.0	1.6	1.8	4.6	3.9	1.9	2.7	5.8	8.2
14.0	8.1	5.7	1.8	2.1	4.9	4.1	1.9	2.5	6.2	8.8
14.4	8.4	5.6	1.4	1.8	5.2	4.2	2.1	2.6	5.7	9.1
15.2	9.2	6.2	1.8	2.0	5.2	4.4	2.1	2.9	6.3	10.0
16.0	9.3	6.2	2.0	2.0	5.2	4.8	2.2	2.9	7.1	10.0
16.4	9.8	6.7	1.8	2.5	5.7	4.7	2.3	3.2	7.1	10.5
16.9	10.0	6.8	1.9	2.3	5.9	4.8	2.4	3.1	7.3	10.8
17.6	10.6	6.7	2.1	2.2	6.1	4.9	2.3	3.5	7.1	11.3
18.6	12.7	-	-	2.8	6.8	5.4	2.8	3.8	8.5	13.2
19.8	12.0	7.7	2.0	2.8	7.1	5.9	2.9	4.0	8.3	13.0
20.0	12.0	8.1	2.2	2.9	7.1	6.4	2.8	4.2	8.4	13.0
20.3	12.8	8.2	1.8	3.1	7.2	6.2	7.8	4.0	8.1	13.5
21.0	13.5	8.6	1.9	3.1	7.5	6.5	3.0	4.6	8.1	14.4
21.4	12.8	8.3	2.4	2.9	7.1	6.2	2.8	3.8	8.6	14.4
21.9	12.8	8.5	2.1	3.1	7.1	6.2	2.8	4.2	8.8	14.9
22.3	14.2	9.6	-	2.8	7.9	6.5	3.2	4.4	9.1	15.4
22.9	14.4	9.8	2.6	3.2	7.5	6.7	3.1	4.6	9.3	15.5
23.2	14.7	9.5	2.5	2.9	7.9	7.2	3.0	5.0	9.6	16.0
23.4	14.9	9.0	2.2	3.3	8.0	7.1	3.2	5.0	9.3	16.4
24.0	14.4	9.8	2.2	3.2	8.0	6.8	3.3	5.0	9.8	15.9
24.3	15.5	10.0	2.8	3.2	8.6	7.3	3.3	5.0	9.8	16.9
25.1	15.9	10.0	3.0	3.3	8.4	7.0	3.4	5.0	10.1	17.2
25.5	16.0	10.1	2.8	3.5	8.8	8.2	3.7	5.5	10.1	17.6
26.4	17.9	10.6	3.2	3.5	9.0	8.0	3.7	5.7	11.3	19.1
27.2	17.9	11.2	3.0	-	8.3	8.1	3.3	5.4	10.8	19.3
*22.5	13.0	8.7	2.1	3.2	7.2	6.3	2.9	4.6	9.6	14.7
*25.3	16.9	10.3	3.5	3.2	8.1	6.8	3.3	5.0	11.2	18.9
*37.8	22.0	12.7	2.9	5.0	10.1	9.6	4.2	8.2	13.5	24.3
*39.0	24.0	14.1	4.0	5.1	9.9	9.8	4.0	8.8	15.0	26.7
*40.8	25.1	14.8	3.8	5.3	10.0	9.7	3.8	8.8	15.3	27.3
*42.3	27.7	15.4	4.3	5.8	10.1	10.0	4.2	9.0	16.3	29.6
*43.6	26.3	15.4	4.1	5.8	9.5	10.6	4.4	9.4	16.1	29.5
*44.7	26.2	15.9	4.3	5.8	11.2	10.5	4.8	8.1	16.9	29.7
*46.2	28.1	16.2	4.4	6.4	10.8	10.8	4.7	9.9	16.7	31.2
*48.8	29.1	16.8	4.7	6.5	11.4	11.4	4.7	10.5	18.0	32.9
*50.3	29.4	17.4	4.8	7.0	12.4	12.2	5.0	10.6	18.0	33.0
*51.0	30.6	17.5	5.0	6.8	11.8	11.5	5.2	10.5	17.5	33.6
*59.2	36.6	20.6	5.4	8.4	13.0	13.5	5.6	12.1	20.8	40.0
*60.0	36.8	21.6	5.7	9.0	14.3	14.3	5.9	13.0	21.5	39.7

* Benthic juvenile.

TABLE 4.—Measurements (mm) of pelagic juveniles of *Sebastolobus macrochir*.

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-dorsal fin	Snout-anal fin
21.0	14.5	9.2	2.5	3.1	9.1	9.2	3.8	5.4	10.0	15.0
25.5	17.9	10.8	3.0	4.5	11.2	11.2	4.7	7.1	11.3	18.2
27.2	18.6	11.8	3.8	4.3	12.5	11.0	4.8	7.7	12.2	19.1
29.8	19.2	13.2	3.0	5.0	13.2	13.2	5.7	8.5	13.5	20.8

TABLE 5.—Meristics from cleared and stained larvae and juveniles of *Sebastolobus* spp. (above dashed line) and *Sebastolobus altivelis* (below dashed line).

Length (mm)	Primary caudal fin rays		Secondary caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right	Superior	Inferior	Upper limb	Lower limb			Left	Right	
6.2	-	-	-	-	5	5	-	-	-	-	-	-	-	-	-	-	-
6.8	-	-	-	-	3	3	14	2	-	-	-	3	-	-	-	-	-
7.0	8	7	-	-	5	5	14	12	-	-	-	2	-	-	-	-	-
7.7	8	7	4	4	7	7	23	24	2	1	3	9	III-5	XV-9	I-5	I-5	28
8.1	8	7	-	2	7	7	23	23	-	-	3	9	III-3	XV-9	I-5	I-5	28
8.3	8	7	3	4	7	7	23	23	2	1	2	8	III-5	XV-9	I-5	I-5	27
8.8	8	7	4	5	7	7	23	24	2	2	3	10	III-5	XV-9	I-5	I-5	29
9.3	8	7	3	4	7	7	24	24	2	1	3	10	III-5	XV-9	I-5	I-5	29
10.1	8	7	6	8	7	7	23	23	1	2	5	12	III-5	XV-9	I-5	I-5	29
10.6	7	7	6	7	7	7	23	23	1	2	5	13	III-6	XV-10	I-5	I-5	29
11.2	8	7	6	7	7	7	23	23	1	2	5	13	III-5	XV-9	I-5	I-5	28
11.5	8	7	7	7	7	7	23	23	1	2	5	13	III-5	XV-9	I-5	I-5	29
12.0	8	7	6	7	7	7	23	23	2	2	5	13	III-5	XV-8	I-5	I-5	28
13.0	8	7	6	7	7	7	23	24	2	2	6	13	III-5	XV-10	I-5	I-5	29
13.7	8	7	6	7	7	7	23	23	2	2	5	13	III-5	XV-9	I-5	I-5	29
14.4	8	7	7	7	7	7	23	24	2	2	6	14	III-5	XV-9	I-5	I-5	29
15.0	8	7	7	7	7	7	23	23	2	2	6	13	III-5	XV-9	I-5	I-5	29
16.6	8	7	7	7	7	7	23	23	2	2	7	14	III-5	XV-9	I-5	I-5	29
17.6	8	7	8	7	7	7	23	23	2	2	7	14	III-5	XV-9	I-5	I-5	29
18.1	8	7	7	7	7	7	24	23	2	2	7	14	III-5	XV-9	I-5	I-5	29
19.4	8	7	7	7	7	7	22	22	2	2	6	14	III-5	XV-9	I-5	I-5	29
20.6	8	7	8	8	7	7	23	23	2	2	7	14	III-5	XV-9	I-5	I-5	29
25.8	8	7	8	9	7	7	24	23	2	2	6	15	III-5	XV-9	I-5	I-5	29
30.5	8	7	6	7	7	7	24	24	2	2	7	15	III-5	XVI-9	I-5	I-5	29
40.4	8	7	7	7	7	7	23	23	2	2	7	15	III-5	XV-9	I-5	I-5	29
50.0	8	7	7	7	7	7	23	23	2	2	7	14	III-5	XV-8	I-5	I-5	29

TABLE 6.—Meristics from cleared and stained larvae and juveniles of *Sebastolobus alascanus*.

Length (mm)	Primary caudal fin rays		Secondary caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right	Superior	Inferior	Upper limb	Lower limb			Left	Right	
7.5	8	7	3	4	7	7	21	21	2	2	3	9	III-5	XVI-8	I-5	I-5	30
11.0	8	7	3	5	7	7	22	22	1	2	4	9	III-5	XVI-9	I-5	I-5	30
11.7	8	7	6	6	7	7	22	22	2	2	4	10	III-5	XVI-8	I-5	I-5	30
12.5	8	7	7	8	7	7	21	21	2	2	5	12	III-5	XVI-10	I-5	I-5	30
13.2	8	7	8	7	7	7	21	22	2	2	5	12	III-5	XVI-9	I-5	I-5	30
14.4	8	7	9	9	7	7	22	22	2	2	5	13	III-5	XVI-9	I-5	I-5	30
15.2	8	7	8	8	7	7	22	22	2	2	5	12	III-5	XVI-9	I-5	I-5	30
16.4	8	7	9	9	7	7	21	21	2	2	7	13	III-5	XVII-9	I-5	I-5	30
17.6	8	7	9	9	7	7	21	21	2	2	6	13	III-5	XVI-9	I-5	I-5	30
18.6	8	7	9	9	7	7	22	22	2	2	6	13	III-5	XVI-9	I-5	I-5	30
19.8	8	7	8	8	7	7	22	22	2	2	6	13	III-5	XVI-9	I-5	I-5	30
20.3	8	7	9	8	7	7	22	22	2	2	5	13	III-5	XVI-9	I-5	I-5	31
21.4	8	7	8	8	7	7	22	22	2	2	6	13	III-5	XVI-9	I-5	I-5	30
22.3	8	7	8	8	7	7	22	22	2	2	6	12	III-5	XVI-9	I-5	I-5	30
24.3	8	7	9	8	7	7	21	21	2	2	7	14	III-4	XVI-9	I-5	I-5	30
25.5	8	7	9	9	7	7	22	22	2	2	6	14	III-5	XV-10	I-5	I-5	30
26.4	8	7	9	9	7	7	21	21	2	2	7	12	III-5	XV-9	I-5	I-5	30
27.2	8	7	10	10			21	21	2	2	7	13	III-5	XVI-10	I-5	I-5	30

DESCRIPTION OF DEVELOPMENT

Distinguishing Features

Early *Sebastolobus* larvae (up to 6 mm) can be distinguished from those of all other genera of eastern Pacific Scorpaenidae on the basis of pigmentation. *Sebastolobus* larvae of this size range are unique in having two large melanistic blotches about midway along the tail, one at the dorsal midline and one at the ventral midline (Figure 1A, B). These are sometimes expanded to form a solid band on the tail. Early larvae of all other eastern Pacific scorpaenid genera have a series of melanophores along the ventral midline of the tail, and in some species of *Sebastes* an opposing row is present at the dorsal midline. The large tail blotches of *Sebastolobus* disappear in larvae between 5.0 and 6.5 mm. Soon after the loss of these large tail blotches in *Sebastolobus* the larvae develop prominent crestlike parietal ridges that terminate in double spines, the posterior (nuchal) spine being longer and more prominent than the anterior (parietal) spine (Figure 1F). Of the other eastern Pacific scorpaenid genera, only the larvae of *Scorpaenodes* have parietal ridges and spines like *Sebastolobus*. If two spines are present on the parietal ridges of other genera, the anterior spine is always longer and more prominent than the posterior. *Sebastolobus* larvae may be distinguished from those of *Scorpaenodes* on the basis of a melanistic shield, which covers the dorsolateral surface of the gut in the former and is absent in the latter. Larvae of *Sebastolobus* smaller than 10.0 mm could not be distinguished to species. Larvae larger than this can be identified to species by a combination of characters. The pectoral fins of *S. altivelis* larvae are relatively longer and are wider at the base than in *S. alascanus*. Also, larvae of *S. altivelis* are deeper bodied than those of *S. alascanus*. Details of the structural and pigmentary characters that differentiate the larvae and juveniles of the two species are given below.

General Morphology

Sebastolobus larvae hatch and are freed from their transparent gelatinous egg masses at about 2.6 mm (Pearcy, 1962). The smallest larvae in our plankton collections are about 3.0 mm long and still have the elliptical yolk sac with a posteriorly positioned oil droplet (Figure 1A). When the larvae reach approximately 3.5 mm, the yolk sac has been resorbed and the jaws and feeding apparatus are well formed (Figure 1B). Flexion of the notochord begins in larvae about 6.0 mm long and is completed in larvae about 7.5 mm (Figure 1E, F). Larvae larger than 10.0 mm and pelagic and benthic juveniles can be identified to species on the basis of characters mentioned above (Figures 2-7). In both species, transformation into the pelagic juvenile stage is initiated within the size range of 14.0 to 20.0 mm. All specimens larger than 20.0 mm have some juvenile pigmentation. The largest pelagic juvenile of *S. alascanus* encountered was 27.2 mm, whereas the smallest benthic juvenile was 22.5 mm. In contrast, in the protracted pelagic juvenile stage of *S. altivelis*, individuals may attain 56.0 mm in length. The smallest benthic juvenile of this species in the collection was 42.0 mm. Pelagic juveniles of *S. macrochir* are similar in shape and pigmentation to those of *S. altivelis*. Although the largest pelagic specimen available was only 30 mm long, it is probable that pelagic juveniles of *S. macrochir* grow larger than this and have a protracted mid-water life as in *S. altivelis*.

Relative body depth (maximum body depth/standard length) changes markedly during development and is an important taxonomic character in the pelagic juveniles (Figure 8). It is 15% at the beginning of the larval period, almost doubles by the onset of notochord flexion, and averages 28% during flexion. It increases further to 35% in larvae 7.5 to 10.0 mm. Relative body depth remains at about this percentage in larvae and pelagic juveniles of *S. alascanus* but decreases sharply to an average of 25% (range of 22 to 32%) in benthic juveniles. Late-stage larvae and pelagic juveniles of *S. altivelis* are much more robust and deeper bodied, averaging 41% (range of 36 to 45%) in the 10- to 40-mm size range. Pelagic juveniles 40 to 50 mm long begin to show a decrease in body depth (mean 38%; range of 36 to 41%), 50- to 55-mm specimens show a further decrease (mean 35%; range of 34 to 37%) and the decrease is precipitous in benthic juveniles (mean 28%; range of 27 to 30%). Body depth in 21- to 30-mm pelagic juveniles of *S. macrochir* averaged 37.5% of the body length (range of 34 to 42%).

The gut has an unusual shape in early larvae up to about 5.5 mm. The narrow, dorsally positioned esophagus runs posteriad from the head for some distance before entering the principal mass of the gut. The effect of this is to produce a space between

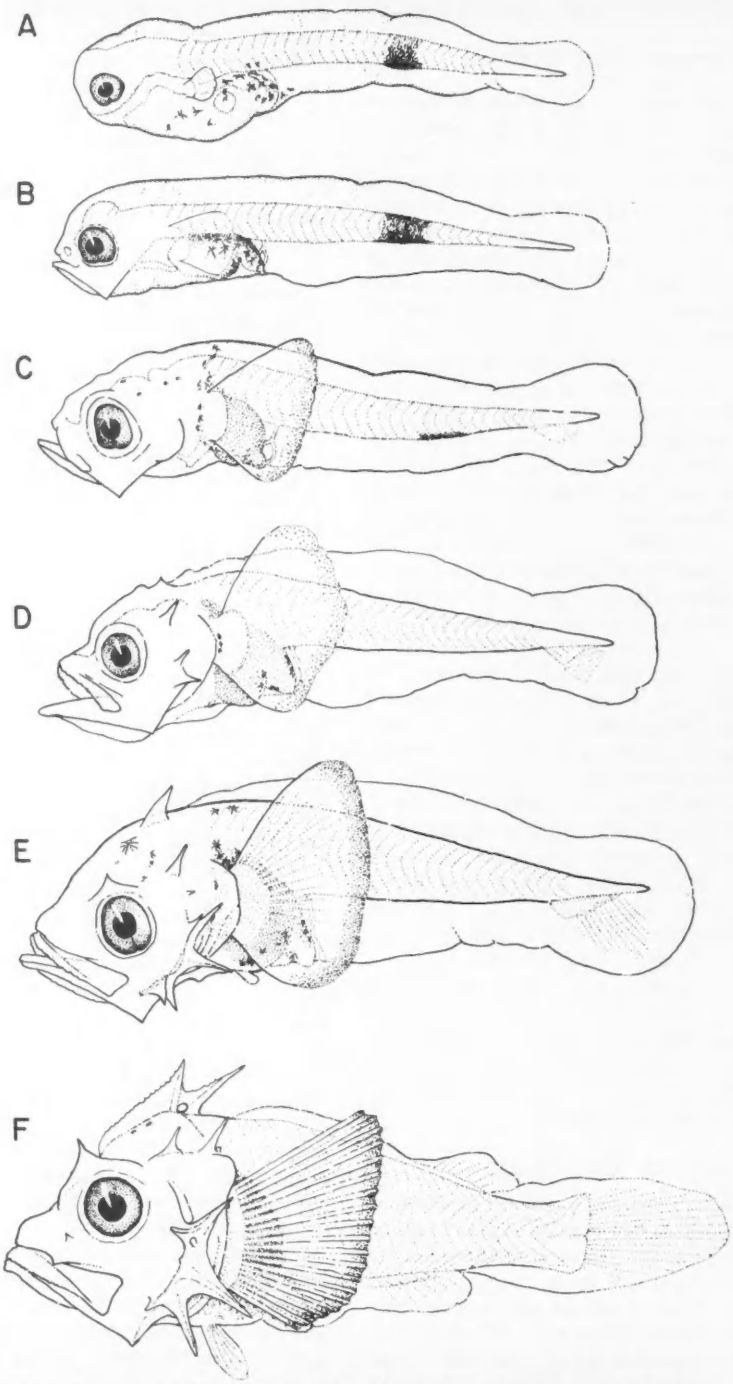

FIGURE 1.—Larvae of *Sebastolobus* spp. from CalCOFI plankton samples. A. 3.0 mm; B. 3.5 mm; C. 5.2 mm: D. 5.7 mm: E. 6.2 mm; F. 7.7 mm.

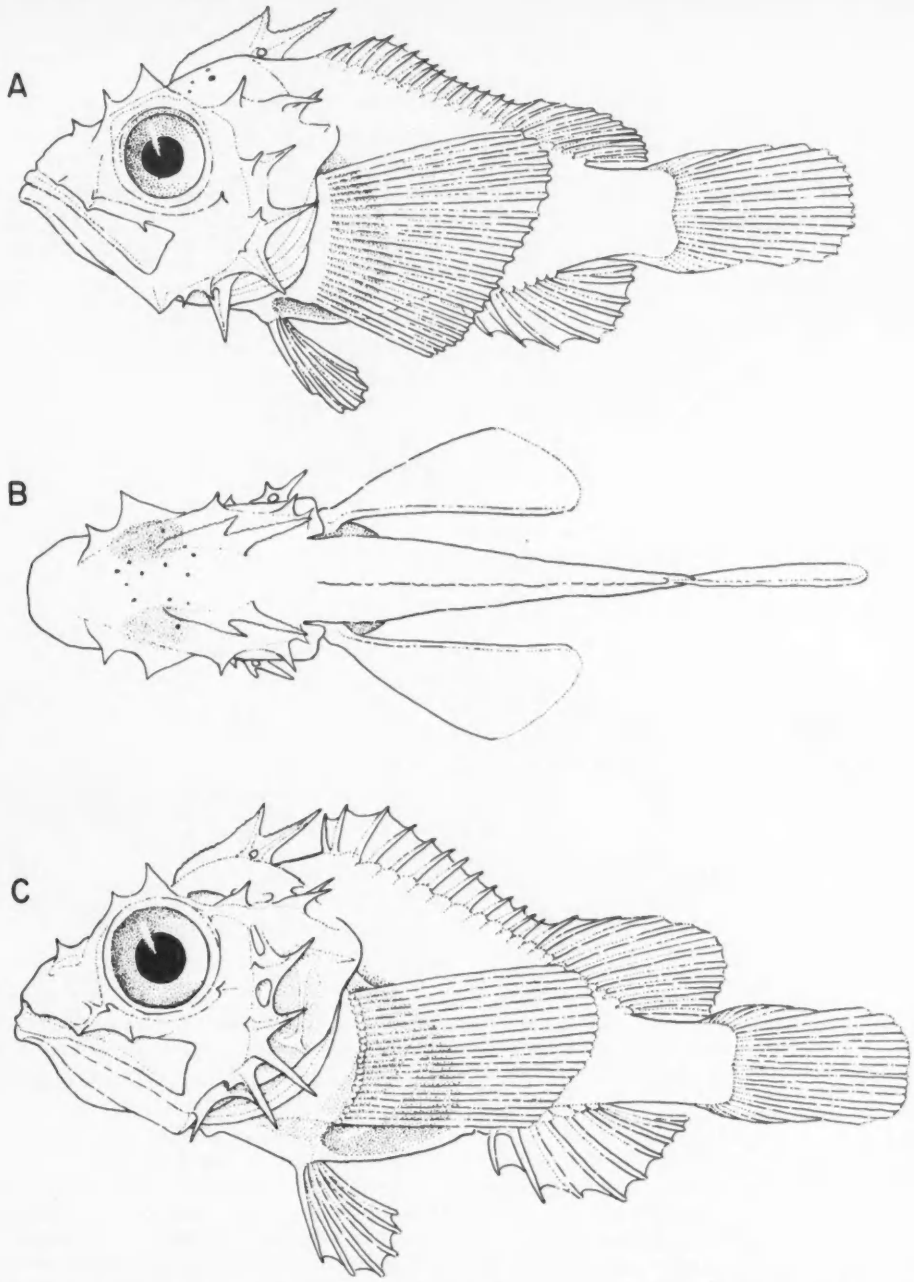

FIGURE 2.—Larvae of *Sebastolobus altivelis* from CalCOFI plankton samples. A. 11.2 mm; B. 11.2 mm, dorsal view; C. 15.4 mm.

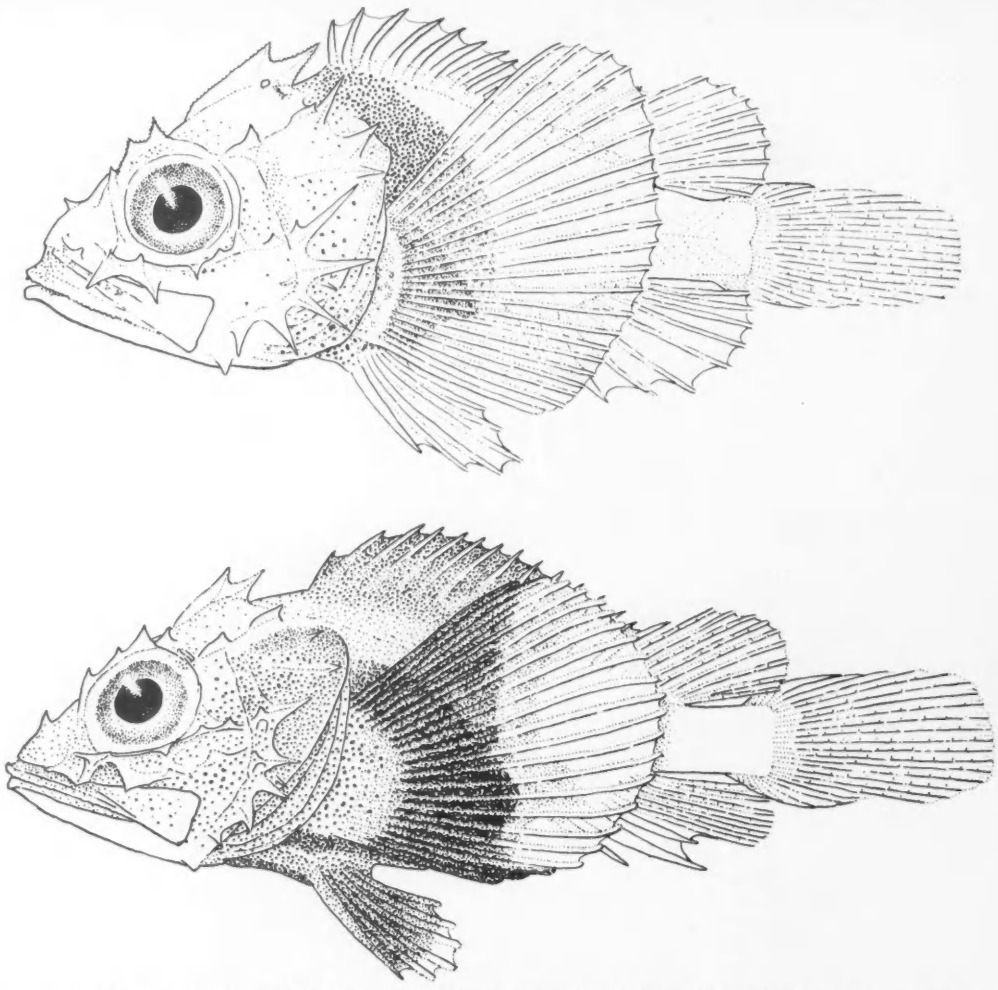

FIGURE 3.—Developmental stages of *Sebastolobus altivelis* from mid-water trawl samples. Above, 16.3-mm transforming specimen. Below, 26.8-mm pelagic juvenile.

the head and the gut (Figure 1B). The space gradually diminishes as the gut enlarges and is absent in larvae larger than 6.0 mm. Relative gut length increases markedly during development. Snout-anus distance averages 41% of the body length up to the stage of notochord flexion, 46% during flexion, and 56% in post-flexion larvae up to 10 mm in length. In larvae and transforming specimens of 10- to 20-mm *S. altivelis* there is an increase to a mean of 64% and in 20- to 56-mm pelagic juveniles there is a further increase to a mean of 68%. In early benthic juveniles snout-anus length averages 64% of body length. The gut is slightly shorter in *S. alascanus;* snout-anus length averages 61% of body length for the larvae and for the pelagic and early benthic juveniles.

The head is moderate in size in early larval stages but enlarges markedly with development. Head length increases from 23% of body length at hatching to an average of 31% during notochord flexion and is 37% in 7.5- to 10.0-mm larvae. Relative head length in larvae and pelagic juveniles of *S. altivelis* in the 10.0- to 40.0-mm size range averages 41%. A slight decrease to a mean of 39%

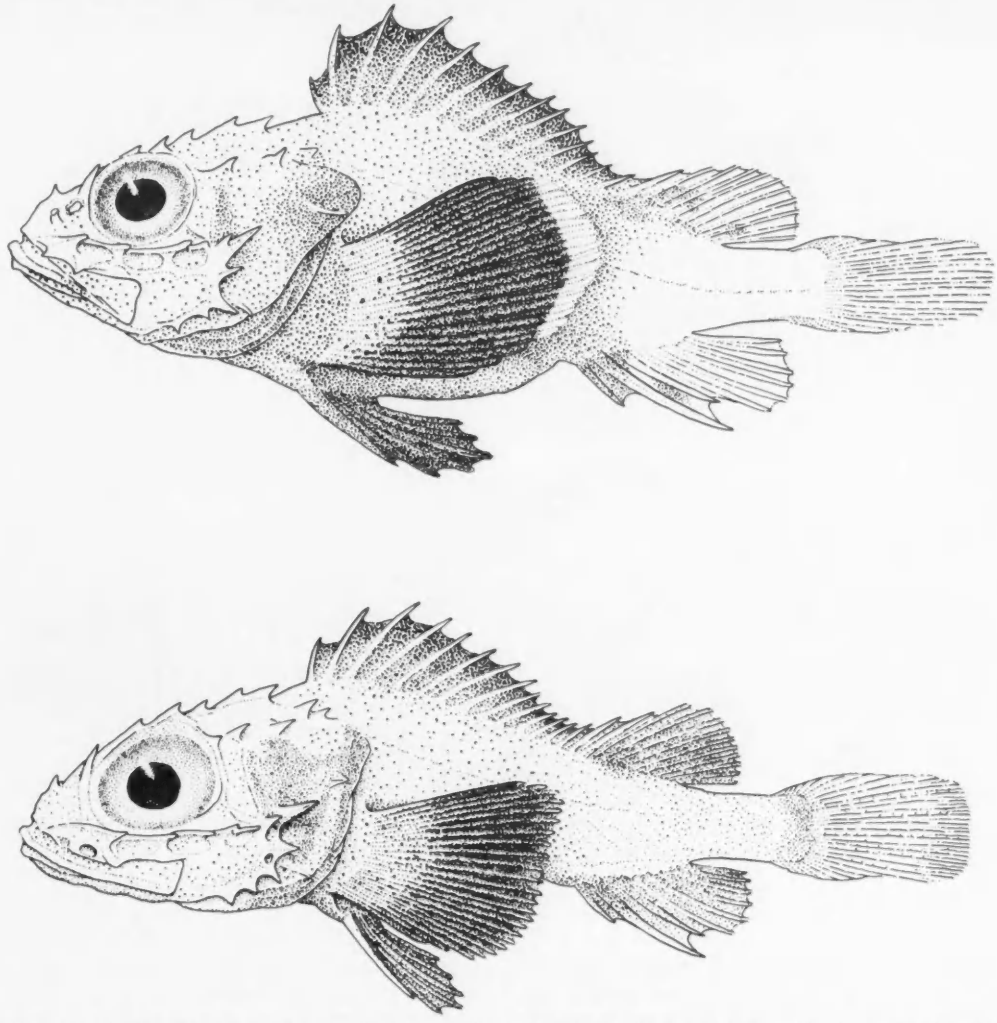

FIGURE 4.—Developmental stages of *Sebastolobus altivelis*. Above, 53.5-mm late pelagic juvenile from mid-water trawl. Below, 53.0-mm benthic juvenile from bottom trawl.

occurs in 40.0- to 56.0-mm specimens and early benthic juveniles average 38%. Virtually the same changes in relative head size occur in *S. alascanus*.

The eyes of early-stage *Sebastolobus* larvae are relatively smaller than in *Sebastes* larvae of comparable size. Eye diameter averages 26% of the head length for larvae up to the beginning of notochord flexion, 27% during flexion, and 28% in post-flexion larvae up to 10.0 mm in length. *Sebastes* larvae average 33 to 35% during comparable stages. Eye diameter in larvae and pelagic juveniles of *S. altivelis* 10.0- to 56.0-mm range) averages 31% of the head length, while in those of *S. alascanus*, eye diameter is slightly larger (mean 33%). In early benthic juveniles of both species, relative eye diameter increases sharply to a mean of 38% of head length. The snout is relatively short in pre-flexion larvae of *Sebastolobus* where snout length averages 27% of head length.

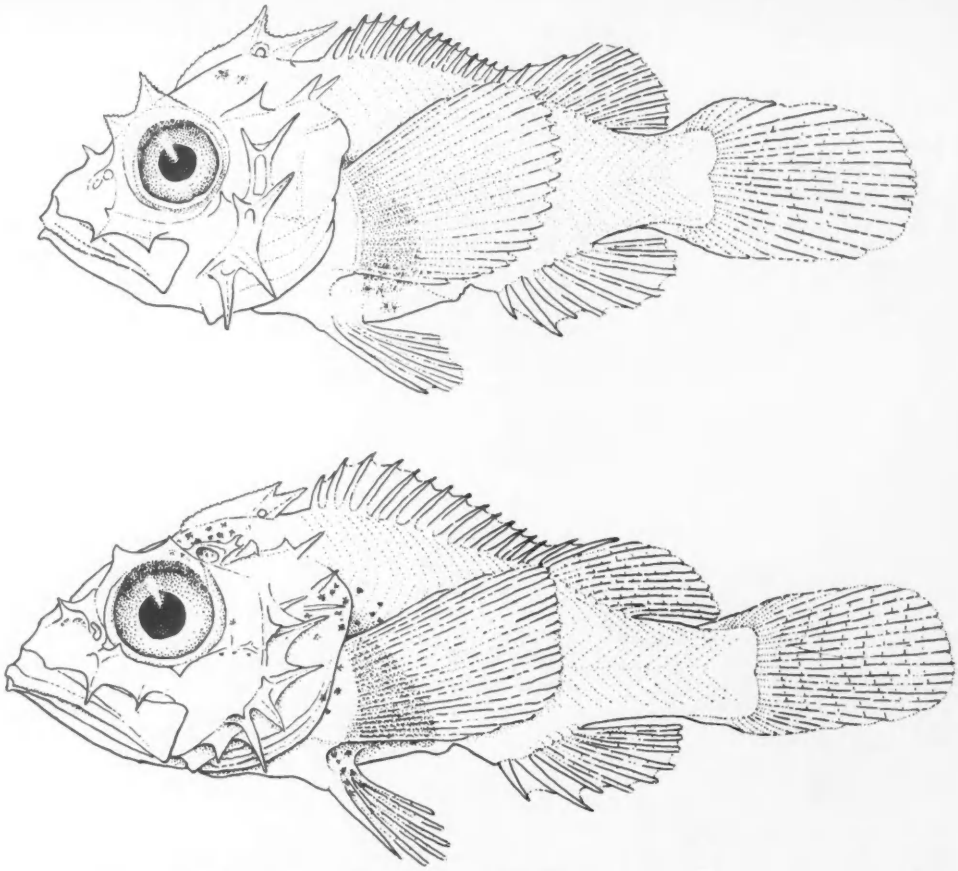

FIGURE 5.—Developmental stages of *Sebastolobus alascanus*. Above, 10.3-mm larva from mid-water trawl. Below, 16.0-mm transforming specimen from mid-water trawl.

This increases to an average 36% in 6.0- to 10.0-mm larvae. Later stages of *S. altivelis* average 28%. *Sebastolobus alascanus* in the 10.0- to 20.0-mm range average 31%, but this is reduced to 27% in the remaining stages.

Fin Development

The pectoral fins of *Sebastolobus* are undifferentiated buds in newly hatched larvae, however, when the larvae reach a length of 3.0 mm the base and blade portions of each fin are beginning to differentiate. From this stage until the initiation of notochord flexion at 6.0 mm the rayed portion of the fin enlarges rapidly to form the large fan-shaped structure characteristic of *Sebastolobus*. At this stage the fin length is about 17% of the body length. This increases to an average of 22% during notochord flexion and 27% in post-flexion larvae up to 10 mm length.

In specimens larger than 10 mm the relative length of the pectoral fin differs considerably between *S. altivelis* and *S. alascanus* (Figure 9). In specimens of *S. altivelis* in the 10- to 20-mm size range, the pectoral fin length averages 34% of the body length (range of 29 to 39%). The pectorals reach their maximum relative length in 20- to 40-mm pelagic juveniles where they average 39% of the body length (range of 35 to 41%). In pelagic juveniles 40 to 50 mm long the average is 35% (range of 32 to 37%), and the fins are still shorter in early benthic juveniles 42 to 60 mm long where they average 29% of the body length (range of 25

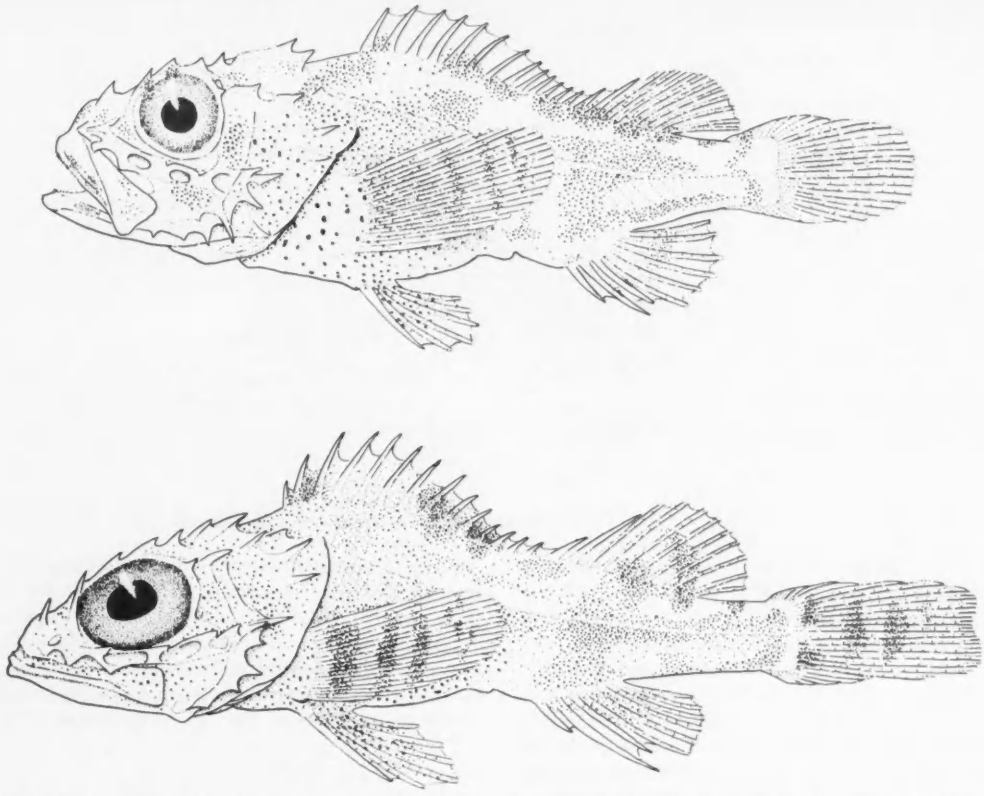

FIGURE 6.—Juveniles of *Sebastolobus alascanus*. Above, 25.3-mm newly transformed benthic juvenile from bottom trawl. Below, 50.3-mm benthic juvenile from bottom trawl.

to 33%). The pectoral fins of *S. alascanus* are considerably shorter than those of *S. altivelis* at comparative sizes. In specimens 10 to 20 mm long fin length averages 29% of body length (range of 26 to 31%). In 10- to 27-mm pelagic specimens pectoral fin length averages 29% of the body length (range of 26 to 32%). In early benthic juveniles 22 to 60 mm long, fin length is reduced to an average of 24% (range of 23 to 28%). The pectoral fin in pelagic juveniles of *S. macrochir* is even longer than in *S. altivelis*. In 21- to 30-mm specimens fin length averaged 43% of the body length (range of 40 to 44%).

The depth of the pectoral fin base is a particularly useful character in distinguishing the larvae of *Sebastolobus* from those of *Sebastes* and is also useful in separating the two species of *Sebastolobus* (Figure 10). In larvae of *Sebastes* examined (e.g., *S. paucispinis*) the depth of the fin base is about 9 or 10% of the body length through notochord flexion; thereafter it gradually diminishes, relative to body length, to about 5 or 6% in the smallest pelagic juveniles. In *Sebastolobus* there is an opposite trend of relative increase from an average of 11% (range of 10 to 15%) in pre-flexion larvae, to 18% (range of 15 to 20%) in subsequent stages of *S. altivelis* up to about 40 mm in length. In larger pelagic juveniles of *S. altivelis* the depth of the pectoral fin base begins to decrease in relation to body length. In 40- to 50-mm specimens the average is 16.5% (range of 15 to 18%) and in 50- to 56-mm pelagic juveniles it is 15% (range of 15 to 16%). It is further reduced to 14% (range of 13 to 15%) in 42- to 60-mm benthic juveniles. The pectoral fin base in *S. alascanus* is significantly shallower

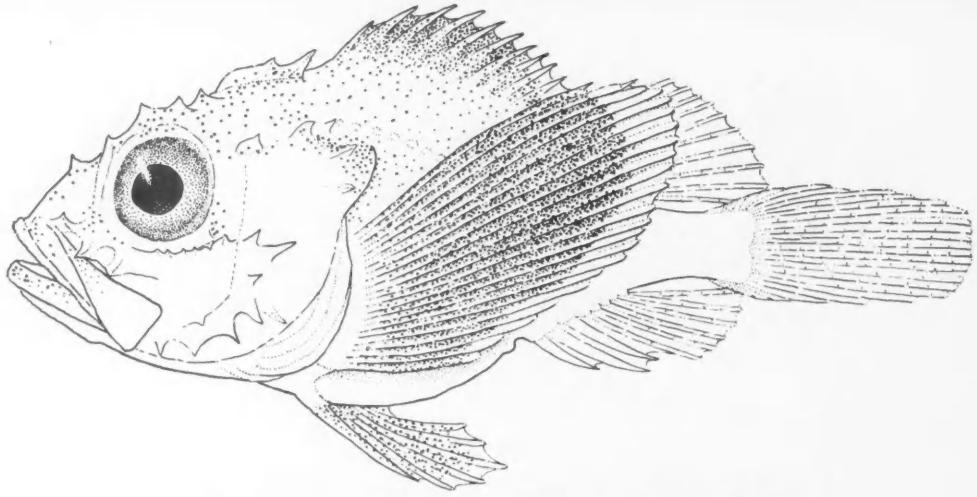

FIGURE 7.—Pelagic juvenile of *Sebastolobus macrochir* from off Kamchatka (27.2 mm).

than in *S. altivelis*. In *S. alascanus* larvae and pelagic juveniles 10 to 30 mm long the fin depth averages 14% of the body length (range of 12 to 16%). In 22- to 60-mm benthic juveniles this is reduced to an average of 10% (range of 9 to 11%).

Ossification of the pectoral fin rays begins in 6.0-mm larvae of *Sebastolobus* (Table 5). The full complements of pectoral rays, 23 to 24 for *S. altivelis* and 21 to 22 for *S. alascanus*, are present in 7-mm larvae (Tables 5, 6).

The pelvic fin buds appear in larvae of about 6.0 mm and elongate to about 12% of the body length by the completion of notochord flexion. Fin length increases to about 17 to 18% of the body length in post-flexion larvae up to 10 mm in length. In *S. altivelis* this increases further to about 24% in pelagic juveniles 20 mm long, and averages 24% (range of 21 to 27%) for the remainder of the pelagic phase. There is a slight decrease to 22% (range of 21 to 24%) in benthic juveniles up to 60 mm long. The pelvic fin is slightly shorter in *S. alascanus* averaging 19% (range of 18 to 20%) in 10- to 20-mm specimens, and 21% (range of 18 to 33%) in larger pelagic juveniles and in benthic juveniles up to 60 mm long. The full complements of one spinous ray and five soft rays are beginning to ossify in 7-mm larvae of *S. altivelis* and *S. alascanus*.

The hypural thickening of the caudal fin first appears in larvae about 3.5 mm long. The hypurals begin to ossify in 7-mm larvae of both species and the full complements of two superior and two inferior elements are ossified in 12-mm larvae of both species. The full complements of eight superior and seven inferior principal caudal rays are beginning to ossify in 7-mm larvae of *Sebastolobus*. The procurrent caudal rays also begin to ossify in 7-mm larvae. The full complements of 6

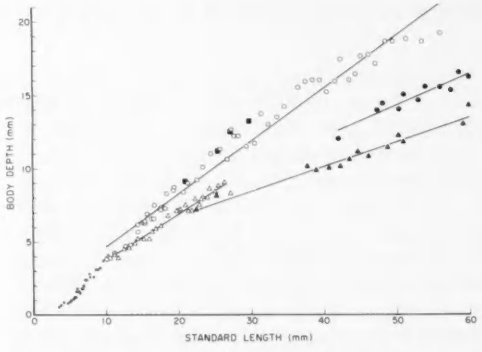

FIGURE 8.—Relationship of body depth to body length in developmental stages of *Sebastolobus*. Small dots = larvae less than 10 mm not identifiable to species. Large open circles = larvae and pelagic juveniles of *S. altivelis*. Large dots = benthic specimens of *S. altivelis*. Open triangles = larvae and pelagic juveniles of *S. alascanus*. Solid triangles = benthic specimens of *S. alascanus*. Solid squares = pelagic specimens of *S. macrochir*. Lines fitted by method of least squares. No regression line drawn for *S. macrochir*.

to 9 superior and 7 to 9 inferior procurrent rays are present in 10-mm larvae of *S. altivelis* and the full complements of 8 to 10 superior and inferior elements are present in 12- to 13-mm larvae of *S. alascanus*.

The dorsal and anal fins begin to develop in 6-mm larvae of *Sebastolobus* and the full complements of rays are ossifying in 7-mm larvae of both species. In *S. altivelis* the usual number of spinous dorsal rays is 15 and in *S. alascanus* the usual number is 16. Both species have 8 to 10 soft dorsal rays with a usual number of 9.

Pigmentation

The melanophore pattern of embryos and yolk-sac larvae of *Sebastolobus* has been described by Pearcy (1962). At the beginning of the larval stage (3.5 mm) the melanophore pattern is distinctive. Large median melanistic blotches oppose each other about midway back on the tail (Figure 1A, B). In some specimens, the blotches are expanded to form a band. Also, melanophores cover the dorsolateral surfaces of the posterior region of the gut. The melanistic tail blotches are transitory; they are lost in some larvae as small as 4.2 mm and one or both are absent in most larvae between 5.0 and 6.0 mm in length. The dorsal spot was absent in all larvae larger than 6.0 mm and the ventral spot was absent in all larger than 6.4 mm. In contrast, the gut pigment is augmented throughout the larval period, extending forward to the axillary region and internally anterior to the cleithrum in larvae about 5.0 mm long. When the larvae reach 6.0 mm the pigment extends onto the ventral surface of the gut and dorsally as deeply embedded pigment at the nape. With continued development the melanophores form a solid sheath on the peritoneum surrounding the gut.

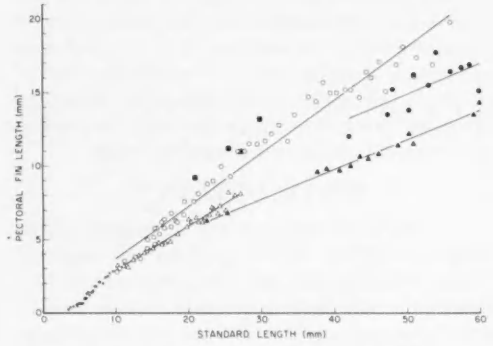

FIGURE 9.—Relationship of pectoral fin length to body length in *Sebastolobus*. Symbols as in Figure 8.

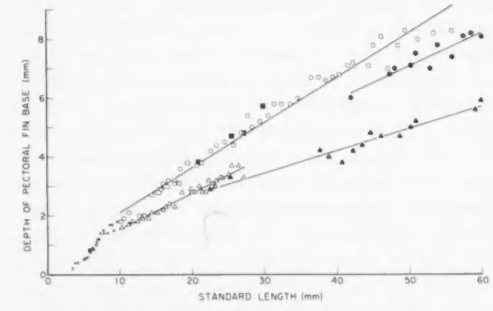

FIGURE 10.—Relationship of depth of pectoral fin base to body length in *Sebastolobus*. Symbols as in Figure 8.

Melanophores appear at the posterior margin of each pectoral fin in some larvae as small as 4.0 mm. About half the larvae examined between 4.0 and 5.0 mm have this posterior margin of fine melanophores and the pigment is present in all larvae in the 5.0- to 11.0-mm range. The melanophores are then lost, and almost all larvae larger than 11.0 mm have pigmentless fins.

Melanophores appear on the posterior lobes of the brain in 5.2- to 7.0-mm larvae and are present in all larvae larger than this. They also appear above the anterior lobes of the brain in larvae between 7.0 and 9.0 mm in length and in most larvae larger than 9.0 mm.

Juvenile pigmentation begins to appear in some specimens of *S. altivelis* of the 14- to 20-mm size range. On the head, patches of melanophores appear on the opercle, cheek, snout, and jaws. In most specimens larger than 22 mm, the patches are confluent, and the head is generally dusky with darker areas at the opercle and along the upper jaw.

A patch of melanophores appears superficially over each side of the gut in specimens as small as 14 mm. These patches expand to form a solid melanistic sheath in some specimens of the 14- to 20-mm size range. The posterior margin of the sheath is an arc running from the vent to the nape and stands out sharply against the pigmentless region of the trunk posterior to the sheath. With continued development the pigment sheath expands posteriad and is a striking feature of the pelagic juveniles. In the 20- to 30-mm size range the sheath extends posteriad to a vertical from the

first or second anal fin spines. In the 30- to 40-mm size range the sheath extends posteriad to the 2nd or 3rd anal spine in most specimens and to the soft dorsal fin in some. In most pelagic juveniles of the 40- to 50-mm size range the dusky sheath extends back to the soft dorsal and it does so in all specimens of the 50- to 60-mm size range. When the juveniles become benthic, the dusky sheath extends posteriad to the caudal fin.

The fins become deeply and characteristically pigmented in juveniles of *S. altivelis*. The anterior portion of the spinous dorsal fin becomes melanistic in specimens as small as 18 mm. In juveniles of the 20- to 25-mm size range the anterior one-half to two-thirds of the fin is melanistic. In the 25- to 30-mm range three-fourths or more of the fin is black. In pelagic juveniles larger than this the pigment has spread onto the soft dorsal fin, and covers both the soft dorsal and soft anal fins in benthic juveniles.

The bases of the pectoral fins begin to be covered with melanophores in specimens as small as 14 mm. In specimens as small as 18 mm the melanophores extend onto the basal region of the rays. With further growth this black basal zone enlarges posteriad and becomes a highly characteristic feature of the pelagic juveniles. The posterior margin of this zone contrasts sharply with the distal clear region of the fin. In juveniles of the 19- to 25-mm size range the width of the black basal zone averaged 20% of the fin length. Enlargement of this zone is shown by the average relative widths for successive size ranges (25 to 30 mm, 38%; 30 to 35 mm, 46%; 35 to 40 mm, 54%; 40 to 45 mm, 65%; 45 to 50 mm, 72%; 50 to 55 mm, 76%). Towards the end of the pelagic juvenile stage a pale translucent layer covers the basal region of the pectoral fin and thus gives the black zone the appearance of a band. The huge pectoral fins, each with their broad black band, are distinctive features of the pelagic juveniles of *S. altivelis*. When the juveniles become benthic the black zone extends to the tips of the fins. Like the pectoral fins, the pelvic fins also develop a black-pigment zone that enlarges with development. In 20- to 25-mm juveniles the basal one-quarter to three-quarters of each fin may be black, although in the majority of specimens the basal one-half is black. In the 25- to 30-mm range most specimens have three-fourths or more of the fin black and in juveniles larger than 30 mm either the fin is entirely black or the extreme tips of the rays are pigmentless.

Juvenile pigment begins to appear in *S. alascanus* in the 14- to 20-mm size range. The first head pigment to appear is a melanistic blotch on the posterior region of the opercle. This gradually spreads anteriorly onto the cheek and in late-stage pelagic juveniles the entire head is speckled with melanophores. A blotch begins to form over each side of the gut in larvae as small as 15 mm. These enlarge dorsad onto the spinous dorsal fin and posteriad as an irregular mottled sheath that contrasts markedly with the solidly pigmented sheath of *S. altivelis* juveniles. In the largest pelagic juveniles the mottling on the dorsal fin and trunk extends posteriad to a vertical from the vent. When the juveniles become benthic the mottling spreads onto the remainder of the body and median fins. Melanophores appear on the bases of the pectoral fins in specimens of the 14- to 20-mm size range. A faint band of melanophores appears on the rays in some specimens of this size range but never becomes highly developed and covers only the basal one-third of the fin in the largest pelagic juveniles. Likewise a faint band of pigment develops on each pelvic fin in specimens as small as 16 mm and only covers the basal half of the fin in the largest pelagic juveniles. When the juveniles become benthic the pectoral fins develop a pattern of four narrow irregular bands.

DISTRIBUTION

The genus *Sebastolobus* has an exceptionally wide latitudinal distribution in the eastern Pacific. *Sebastolobus altivelis* ranges from the Aleutian Islands southward to Cape San Lucas, Baja California, and *S. alascanus* inhabits waters from the Bering Sea to northern Baja California (Barsukov, 1964; Miller and Lea, 1972). The extensive north-south range of *Sebastolobus* is probably related to habitat depth rather than eurythermy. They are deep-living species throughout their latitudinal range and, as such, experience little change in habitat temperature towards the southern end of their range. Alverson et al. (1964) reported that significant catches of *Sebastolobus* are taken at depths shallower than 150 fathoms in the trawl fishery from Oregon to southeastern Alaska, but that the percentage contribution of *Sebastolobus* increased with depth. At the maximum depth range sampled, 500 to 600 fathoms, *Sebastolobus* accounted for about 70% of the total fish catch. Southward of Oregon the shoaler elements of the *Sebastolobus* populations are gradually eliminated and, off

southern California, adults of even the shallower-living species, *S. alascanus,* are generally restricted to waters deeper than 150 fathoms.

Curtailment of spawning or mortality of fertilized eggs off southern California is evident from the distribution of *Sebastolobus* larvae in the CalCOFI sampling area (Figures 11, 12). In 1966, there were no occurrences south of line 97, which runs seaward from the Mexican border, and in 1969 *Sebastolobus* occurred on only two stations below this line. It is apparent that the CalCOFI sampling pattern did not encompass the offshore limits of larval distribution and that larvae occur well seaward of the 200 to 250 mile coastal zone sampled during these years.

The seasonal abundance of *Sebastolobus* larvae for 1966 and 1969 is shown in Table 7. In 1966 larvae were taken from April to October in central and southern California. Numbers of larvae and occurrences were highest in April and diminished in subsequent months. No larvae were taken south of southern California in 1966. In 1969, larvae appeared earlier in the year, from January to December off central California, from January to October off southern California, and from June to September off northern Baja California. Again, numbers of larvae and occurrences peaked in April off central and southern California. Data for the two species are lumped together in Table 7. Of the larvae identifiable to species, those over 10 mm, 6% were *S. alascanus* in 1966 and 12% were *S. alascanus* in 1969. Thus, the data in Table 7 pertain largely to *S. altivelis.*

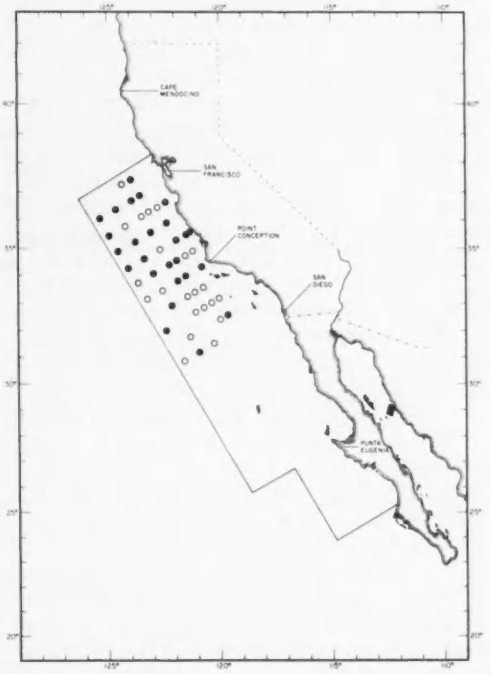

FIGURE 11.—Stations at which larvae of *Sebastolobus* were collected during CalCOFI survey of 1966. Dots indicate stations where numbers of *Sebastolobus* larvae exceeded mean number (7.2) for all positive stations. Area of frequent occupancy is outlined (see Ahlstrom, 1961, for complete grid).

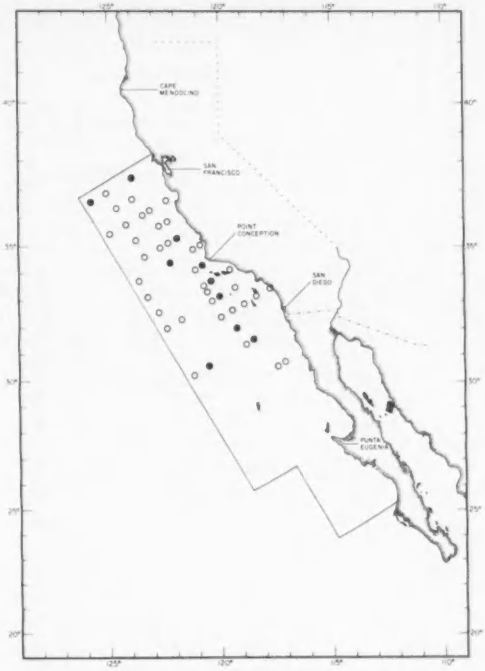

FIGURE 12.—Stations at which larvae of *Sebastolobus* were collected during CalCOFI survey of 1969. Symbols as in Figure 11.

Although *Sebastolobus* larvae are taken in plankton tows over a large proportion of the year, the spawning season is relatively short. Table 8 shows the seasonal change in the size of *Sebastolobus* larvae. The mean size increases steadily throughout the year and small, recently spawned larvae, less than 5 mm, do not occur after June in 1966 and May in 1969. This indicates a spawning season of 4 or 5 mo.

Information on the growth rate of the pelagic juveniles of both species of *Sebastolobus* was obtained by examining mid-water trawl samples

TABLE 7.—Standard numbers and occurrences of *Sebastolobus* larvae taken during 2 yr of the California Cooperative Oceanic Fisheries Investigations. Dashes indicate region not occupied.

		Month																					
		Jan.		Feb.		Apr.		May		Jun.		Jul.		Aug.		Sep.		Oct.		Nov.		Dec.	
	Year	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.
Central California CalCOFI Lines 60–77	1966	-	-	0	0	227	19	0	0	89	14	67	10	0	0	0	0	13	3	-	-	-	-
	1969	3	1	12	4	81	10	10	2	0	0	17	5	38	9	0	0	14	4	-	-	3	1
Southern California CalCOFI Lines 80–93	1966	-	-	-	-	58	10	34	7	3	1	10	3	37	4	39	8	17	3	-	-	-	-
	1969	3	1	3	1	-	-	3	1	0	0	19	6	13	4	-	-	3	1	-	-	-	-
Northern Baja California CalCOFI Lines 97–107	1966	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	1969	-	-	-	-	-	-	0	0	10	2	13	3	0	0	6	2	-	-	-	-	-	-

from the Los Angeles County Museum, Scripps Institution of Oceanography, and the Southwest Fisheries Center. A total of 260 samples from the years 1950 to 1969 were examined. Most of the samples were taken in the deepwater basins off southern California, but two samples of *S. alascanus* were taken as far north as Crescent City, Calif., and one sample of *S. altivelis* was from the vicinity of Guadalupe Island, Baja California.

The composite monthly size frequencies of mid-water trawl specimens of *S. altivelis* are shown in Figure 13. Two major size classes are present from May through September. One class is formed by larvae and transforming specimens, less than 20 mm in length, from the January-May spawning season. The other class is formed

FIGURE 13.—Composite monthly size frequencies for larvae and pelagic juveniles of *Sebastolobus altivelis* from mid-water trawls.

TABLE 8.—Mean lengths with standard deviations in mm (A) and size ranges in mm (B) of *Sebastolobus* larvae taken during 2 yr of the California Cooperative Oceanic Fisheries Investigations.

	Month									
	Jan.		Feb.		Apr.		May		Jun.	
Year	A	B	A	B	A	B	A	B	A	B
1966	-	-	-	-	4.3 ± 1.07	2.2 - 6.9	6.2 ± 1.16	4.2 - 7.8	7.4 ± 1.17	5.1 - 10.0
1969	3.1 ± 0.65	2.8 - 3.4	3.0 ± 0.47	2.8 - 3.4	3.6 ± 0.76	2.6 - 4.7	4.2 ± 0.98	3.1 - 5.2	8.6 ± 0.68	8.1 - 8.9

	Month									
	Jul.		Aug.		Sep.		Oct.		Dec.	
Year	A	B	A	B	A	B	A	B	A	B
1966	8.7 ± 1.15	6.2 - 11.2	11.6 ± 1.42	9.2 - 15.2	14.0 ± 1.57	9.2 - 17.7	16.4 ± 1.37	14.4 - 19.3	-	-
1969	10.8 ± 1.15	8.9 - 13.2	11.8 ± 1.58	9.2 - 18.2	17.0 ± 1.10	16.2 - 17.9	16.3 ± 1.43	15.2 - 18.6	15.0	15.0

by large pelagic juveniles from the previous year's spawning season. A single size class of transforming specimens is present in October and November, however, the absence of the large pelagic juveniles is probably due to inadequate sampling, since they are present in December. From January through April a single class of pelagic juveniles is present. In summary, the early life history of *S. altivelis* is as follows: larvae are produced in a 4- or 5-mo spawning season that peaks in April. Transformation into pelagic juveniles begins as early as July and by the end of December most have completed transformation. The prolonged pelagic juvenile stage lasts until the following summer when the juveniles begin to settle to the bottom. This process probably extends over a 6- to 8-mo period with some juveniles remaining pelagic until December. The total period spent in the pelagic environment from spawning to settling is about 20 mo. The means of the composite monthly length frequencies are plotted in Figure 14 to give an estimation of growth of this species.

The composite monthly length frequencies for mid-water trawl-caught specimens of *S. alascanus* are shown in Figure 15. In contrast to *S. altivelis*, only a single size class is present each month. From July to December a single class of larval and transitional specimens less than 20 mm long is present. Some pelagic juveniles are present in December and by January most of the specimens have completed transformation. Successive samples from February to May contain only pelagic juveniles. In summary, the planktonic and early pelagic life history of *S. alascanus* is similar to that of *S. altivelis*. A probable 4- or 5-mo spawning period that peaks in April gives rise to larvae that appear in mid-water trawl samples in summer. Transformation into the pelagic juveniles begins as early as August and most have completed transformation by the end of December. A class of pelagic juveniles is present from December through May, however, the size ranges for these months overlap the range at which *S. alascanus* juveniles begin to settle to the bottom, and it is

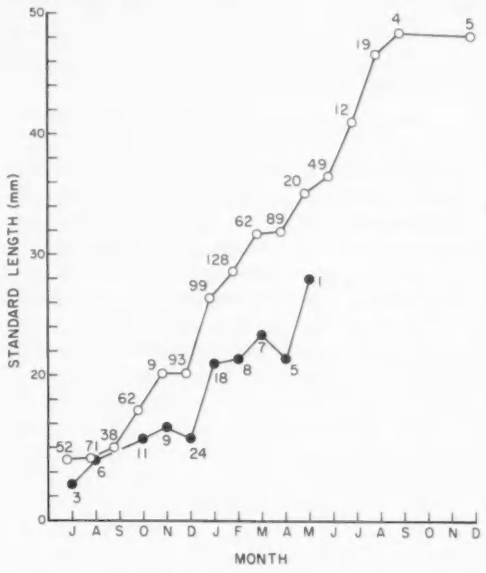

FIGURE 14.—Means of composite monthly size frequencies of larvae and pelagic juveniles of *Sebastolobus altivelis* and *S. alascanus* from mid-water trawls.

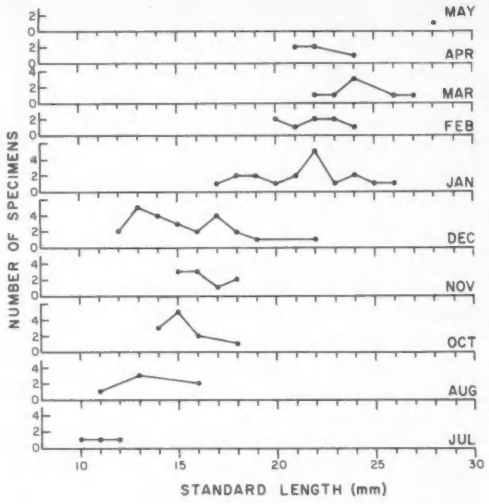

FIGURE 15.—Composite monthly size frequencies for larvae and pelagic juveniles of *Sebastolobus alascanus* from mid-water trawls.

probable that settling begins as early as January. Most have become benthic by May or June. The pelagic juvenile stage in this species is short-lived compared with *S. altivelis* and the total period spent in the pelagic environment from spawning to settling is about 14 or 15 mo. The means of the composite monthly frequencies are plotted in Figure 14.

ACKNOWLEDGMENTS

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SWIMMING ENERGETICS OF THE LARVAL ANCHOVY, *ENGRAULIS MORDAX*

WILLIAM J. VLYMEN III[1]

ABSTRACT

A modification of Gray and Hancock's theoretical method for studying propulsion of spermatozoa was used to estimate the energy expenditure of swimming anchovy, *Engraulis mordax*, larvae. Wave parameters obtained from photographs of feeding anchovy larvae were incorporated into a time dependent sinusoidal body displacement function which is used in the iterated energy integrals of the model. The integrals were numerically evaluated by 2-dimensional 16-point Gaussian-Legendre quadrature. The results for the mean larval length of 1.4 cm was 144.8 ergs/swimming excursion or 4.91×10^{-3} cal/h using known excursion rates. O_2 consumption measurement of similar size larvae indicate a 2.19×10^{-2} cal/h requirement. Extension to other larval sizes can be made using this model with certain qualifications. The relationships of swimming energetics to larval fish behavior are discussed. Current theories of large amplitude intermittent swimming are also discussed in light of the high swimming efficiencies encountered in this study.

The theoretical evaluation of swimming fish energetics by hydrodynamic analysis has been an extensively treated subject in recent years. Most of these treatments however have concentrated on calculation of thrust and thrust efficiencies with the exception of Lighthill (1970, 1971) who gave direct estimates for the mean swimming work rate and has drawn attention to the importance of the accelerative, virtual mass contributions in estimates of mean swimming work rate. Most expositions, however, deal with situations where inertial effects predominate with all subsequent derivations being consistent with that assumption (Taylor, 1952a). The low Reynolds number range of swimming energetics primarily of spermatozoa, has also been extensively treated (Taylor, 1951, 1952b; Gray and Hancock, 1955; Carlson, 1959; Holwill and Miles, 1971). All these treatments disregard inertial and accelerative effects in comparison with viscous effects in their treatment. Also, both viscous and inertial treatments calculate or estimate the mean swimming work rate after steady motion has been established.

The problem attacked in this paper is a synthesis and extension of the two classes of treatments discussed above, specifically to determine the energy expended per excursion by the 1-cm larval anchovy, *Engraulis mordax*. The term excursion as used here requires some elaboration. Larval anchovies have a peculiar swimming behavior because they do not continuously propagate caudally directed waves. In the adult form this behavior is noticeable by observing the tail, i.e., it does not beat continuously even though the fish appears to maintain constant forward motion. In the larval stages, however, this behavior results in an obvious discontinuous motion. The result is a series of bursts of motion from rest to rest which hereafter I refer to as excursions.

The estimation of excursion energetics by a theoretical model rather than indirect metabolic estimators during excursions is demanded because of the small size of the organisms considered, their discontinuous motion, and the investigator's inability to determine which fraction of the total energy consumption is due to swimming alone.

The parameters used in the model to calculate the excursion energy are taken from photographs of a larval anchovy of a specified size executing excursions in search of prey organisms. Since the search for prey constitutes a large proportion of the larva's activity, following Kerr (1971) we can write the total metabolism of the larva as,

$$T_T = T_F + T_C + T_S$$

where T_T = total metabolism
T_F = cost of search for prey

[1]Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. BOX 271, La Jolla, CA 92037 and Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92037.

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T_S = standard metabolism
T_C = internal cost of food utilization.

The growth efficiency and subsequent relations derived from T_T are important in estimating fish yields in relation to standing food resources and other factors important to fisheries management. It is this larger view which gives relevance to the rather involved procedure of simply calculating one part of the value of T_T, namely T_F.

THEORY

The derivation of the excursion energy estimate is based on Gray and Hancock's (1955) development for spermatozoa. Instead of a cylinder with an inert head attached, the anchovy larva is regarded here as a ribbon or plate of specified width attached to an inert head (Figure 1). The assumption that the body is a ribbon is justified only if the ratio of the width to thickness (W/t) is $\gg 1$. In the larvae examined in this study this ratio averaged 2.5. While this ratio is not $\gg 1$ I have assumed that it is to simplify the problem. However, the error introduced is, I believe, minimal.

From Figure 1 the following relation is noted and will be used in the following derivations:

$$V_N = V_y \cos\theta - V_x \sin\theta \qquad (1)$$

$$V_T = V_y \sin\theta + V_x \cos\theta \qquad (2)$$

where V_N = normal velocity of an element of body
V_T = tangential component
V_y = y-component
V_x = x-component.

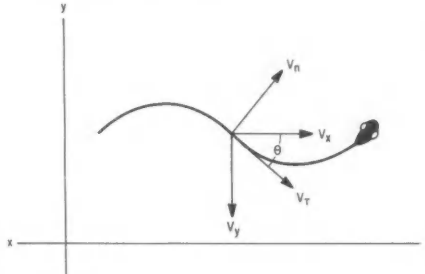

FIGURE 1.—Diagram illustrating the relationship of the velocity components of an element of body when moving transversely in the X-direction.

With the body approximated as an inextensible ribbon we find the use of the normal drag coefficient, C_N, and the tangential drag coefficient, C_T, convenient in addition to an appropriate sagittal contour function $h(s)$ where s denotes distance along the spine of the fish (see Figure 4).

The expression for the velocities V_N and V_T is first expressed in terms of the function which represents the propagated wave along the body $y(x,t)$, and V_x. By noting,

$$V_y = \frac{dy}{dt} \text{ and } \tan\theta = \frac{dy}{dx}$$

we can rewrite Equations (1) and (2) as,

$$\frac{V_N}{\cos\theta} = \frac{dy}{dt} - V_x \frac{dy}{dx} \text{ and } \frac{V_T}{\cos\theta} = \frac{dy}{dt}\frac{dy}{dx} + V_x.$$

$$\text{Given } \cos\theta = \frac{1}{[1 + \tan^2\theta]^{1/2}} = \frac{1}{\left[1 + \left(\frac{dy}{dx}\right)^2\right]^{1/2}}$$

$$\text{we get } V_N = \left[\frac{dy}{dx} - V_x \frac{dy}{dx}\right]\left[1 + \left(\frac{dy}{dx}\right)^2\right]^{-1/2} \qquad (1')$$

$$V_T = \left[\frac{dy}{dt}\frac{dy}{dx} + V_x\right]\left[1 + \left(\frac{dy}{dx}\right)^2\right]^{-1/2} \qquad (2')$$

Now we may proceed to write the contributions to the total work of excursion made by the head, body viscous reactive terms, and accelerative body virtual mass.

The element of work performed in moving the inert head is given by,

$$dW_H = 1/2\,\rho\, C_H\, A\, V_x^3\, dt + (m + M)\frac{dV_x}{dt} V_x\, dt$$

(Vlymen, 1970)

where dW_H = element of work performed by the head
C_H = drag coefficient of the head
A = cross-sectional area
m = virtual mass of head
M = mass of head
ρ = density of seawater.

Thus, given the time of excursion as t_E we get,

$$W_H = 1/2 \int_0^{t_E} (\rho C_H A V_x^3 + 2(m + M)\frac{dV_x}{dt} V_x)dt, \quad (3)$$

The element of work performed by the body contributed by viscous-reactive forces can be approximated using experimental values for the normal and tangential drag coefficient of a smooth plate. The choices made are

$$C_N = \frac{k_N}{Re} = \frac{20.37}{Re} \quad \text{(Hoerner, 1965)} \quad (4)$$

$$\text{and } C_T = \frac{k_T}{\sqrt{Re}} = \frac{1.328}{\sqrt{Re}} \quad \text{(Schlicting, 1960)} \quad (5)$$

where Re is the appropriate Reynolds number respectively. Although these are primarily low Reynolds number approximations they are within 10% at $Re = 30$. Thus F_N, the normal force on a plate of frontal area A is given by

$$F_N = 1/2\, \rho\, C_N V_N^2\, A.$$

Since for any position along the fish body

$$Re = \frac{2V_N h(s)}{\nu}$$

ν the kinematic viscosity, we get using C_N from Equation (4) the normal force dF_N on an element of body ribbon as,

$$dF_N = \frac{\rho k_N \nu}{4V_N h(s)} V_N^2\, 2h(s)\, ds = \frac{\rho}{2} k_N \nu V_N\, ds.$$

In a similar manner F_T, the tangential force on a plate of total wetted surface area A, is

$$F_T = 1/2\, \rho\, C_T V_T^2\, A.$$

Since the formula for C_T above uses $Re = \frac{V_T l}{\nu}$ where l is distance measured along the body, we get the tangential force dF_T on an element of body ribbon as

$$dF_T = \frac{2\rho k_T \sqrt{\nu}}{\sqrt{V_T s}} V_T^2\, h(s)\, ds$$

$$= 2\rho k_T \sqrt{\nu} V_T^{3/2} \frac{h(s)}{\sqrt{s}} ds. \quad (7)$$

Multiplying each element of force above by the element of distance in the direction of that force and summing yields,

$$dW_B^{V.R.} = \frac{\rho}{2} k_N \nu V_N^2\, dsdt + 2\rho k_T \sqrt{\frac{\nu}{s}} V_T^{5/2}\, h(s)\, dsdt$$

where $dW_B^{V.R.}$ is the element of viscous reactive work performed by an element of body ribbon. Using the Equations (1′) and (2′) for V_N and V_T and integrating over the excursion time t_E and projected body length excluding the head we get,

$$W_B^{V.R.} = \frac{\rho}{2} \int_0^{t_E} \int_{l_H}^{l} \left[\frac{k_N \nu \left[\frac{dy}{dt} - V_x \frac{dy}{dx}\right]^2}{\left[1 + \left(\frac{dy}{dx}\right)^2\right]^{1/2}} \right] dsdt + \rho \int_0^{t_E} \int_{l_H}^{l} \frac{2k_T \sqrt{\nu} \left[\frac{dy}{dt}\frac{dy}{dx} + V_x\right]^{5/2} h(s)}{\sqrt{s}\left[1 + \left(\frac{dy}{dx}\right)^2\right]^{3/4}} dsdt.$$

where l_H is the x-projected length of the inert head. Eliminating ds by the relation,

$$ds = \left[1 + \left(\frac{dy}{dx}\right)^2\right]^{1/2} dx$$

yields finally,

$$W_B^{V.R.} = \frac{\rho}{2} \int_0^{t_E} \int_{l_H}^{l} \left[\frac{k_N \nu \left[\frac{dy}{dt} - V_x \frac{dy}{dx}\right]^2}{\left[1 + \left(\frac{dy}{dx}\right)^2\right]^{1/2}} \right] dxdt + \rho \int_0^{t_E} \int_{l_H}^{l} \frac{2k_T \sqrt{\nu} \left[\frac{dy}{dt}\frac{dy}{dx} + V_x\right]^{5/2} h(s)}{\sqrt{s}\left[1 + \left(\frac{dy}{dx}\right)^2\right]^{3/4}} dxdt.$$

As will be noted s is present in the second of the

integrals above; however, later in the discussion s and $h(s)$ will be converted to appropriate functions of x and t so that the integrations may be performed.

The accelerative or virtual mass element of work can be calculated using the fact that the virtual mass of a flat plate accelerating parallel to its normal vector is equal to the mass of the fluid enclosed in a circumscribing cylinder having the plate chord as diameter (Fung, 1969). Hence from Figure 2 the virtual mass is given by

$$dM = \rho \pi h^2(s)\, ds$$

and the magnitude of the acceleration by

$$a \sin \theta_1 = a \sin(\theta - \theta_2)$$

where $a = \left| \tilde{a} \right|$.

Now $\theta = \tan^{-1} \frac{dy}{dx}$ and $\theta_2 = \tan^{-1} \frac{V'y}{V'x}$

where $V'y = \frac{dVy}{dt}$ and $V'x = \frac{dVx}{dt}$, giving

$$a \sin(\theta - \theta_2) = a \sin\left(\tan^{-1} \frac{dy}{dx} - \tan^{-1} \frac{V'y}{V'x}\right)$$

Since $\left| \tilde{a} \right| = \left(V'^2_y + V'^2_x \right)^{1/2}$, we get

$$a \sin(\theta - \theta_2) = \left(V'^2_y + V'^2_x \right)^{1/2} \cdot \sin\left(\tan^{-1} \frac{dy}{dx} - \tan^{-1} \frac{V'y}{V'x} \right)$$

Thus the magnitude of force $F_{V.M.}$ on an element of body ribbon due to induced mass dM is

$$\left| F_{V.M.} \right| = a\,dM = \rho \pi h^2(s)(V'^2_y + V'^2_x)^{1/2} \cdot \sin(\tan^{-1} \frac{dy}{dx} - \tan^{-1} \frac{V'y}{V'x}).$$

Since the element of work is given by

$$dW = \left| F_{V.M.} \right| \cdot \left| dx \right| \cdot \cos(F_{V.M.} \left| dx \right)$$

where

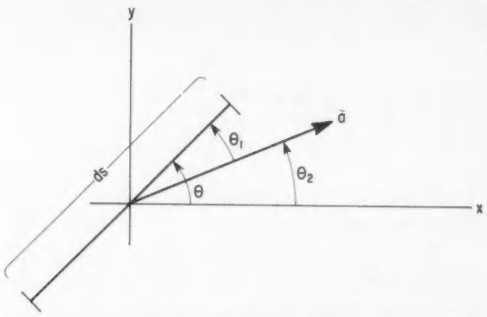

FIGURE 2.—Diagram illustrating body element undergoing acceleration $\tilde{a}$ and relationships of orientation of element to vector $\tilde{a}$ in terms of the angles θ, θ_1, θ_2.

$$\left| dx \right| = (V_y^2 + V_x^2)^{1/2}\, dt$$

and

$$\cos(F_{V.M.} \left| dx) = \cos(\tan^{-1} \frac{V'y}{V'x} - \tan^{-1} \frac{Vy}{Vx}),$$

we get finally

$$dW = \rho \pi h^2(s) (V_y^2 + V_x^2)^{1/2} \quad (V'^2_y + V'^2_x)^{1/2} \cdot \sin\left(\tan^{-1} \frac{dy}{dx} - \tan^{-1} \frac{V'y}{V'x} \right) \cdot \cos\left(\tan^{-1} \frac{V'y}{V'x} - \tan^{-1} \frac{Vy}{Vx} \right) ds dt.$$

Using the identities for $\cos(a - b)$, $\sin(a - b)$, and ds gives finally,

$$dW^A_{B_I} = \frac{\rho \pi h^2(s) \left[\frac{dy}{dx} V'x - V'y \right] \left[V'x\ Vx + \frac{dy}{dt} \frac{d^2y}{dt^2} \right] dx dt}{\left[V'^2_x + \left(\frac{d^2y}{dt^2} \right)^2 \right]^{1/2}}$$

where $dW^A_{B_I}$ is part I of the element of work performed by the acceleration of the surrounding fluid.

In addition to $dW^A_{B_I}$ above we also want the work done in accelerating the body itself. Calling $\rho_B(s)$ the linear mass density of the body we get, using Figure 2,

$$dW^A_{B\,II} = \rho_B(s)\left(V'^2_x + \left(\frac{d^2y}{dt^2}\right)^2\right)^{1/2} \cdot \left(V^2_x + V^2_y\right)^{1/2} \cdot \cos\left(\tan^{-1}\frac{V'y}{V'x} - \tan^{-1}\frac{Vy}{Vx}\right) dsdt$$

where $\left(V'^2_x + \left(\frac{d^2y}{dt^2}\right)^2\right)^{1/2} = \left|a\right|$,

$\left(V^2_x + V^2_y\right)^{1/2} dt = \left|dx\right|$,

$\rho_B(s)\, ds = dm.$

When the above terms are expanded we get, taking account of ds,

$$dW^A_{B\,II} = \rho_B(s)\left(Vx\, V'x + \frac{dy}{dt}\frac{d^2y}{dt^2}\right)\left(1 + \left(\frac{dy}{dx}\right)^2\right)^{1/2} dxdt.$$

Integrating $dW^A_{B_I} + dW^A_{B\,II}$ from 0 to t_E in t and l_H to l in x we get the accelerative body work,

$$W^A_B = \int_0^{t_E}\int_{l_H}^{l} \rho_B(s)\left(Vx\, V'x + \frac{dy}{dt}\frac{d^2y}{dt^2}\right)\left(1 + \left(\frac{dy}{dx}\right)^2\right)^{1/2} dsdt \qquad (8)$$

$$+ \rho\int_0^{t_E}\int_{l_H}^{l} \pi h^2(s)\frac{\left[\frac{dy}{dx}V'x - V'y\right]\left[Vx\, V'x + \frac{dy}{dt}\frac{d^2y}{dt^2}\right]}{\left[V'^2_x + \left(\frac{d^2y}{dt^2}\right)^2\right]^{1/2}} dxdt.$$

The total work estimated per excursion is then given by the sum of W^A_B, $W^{V.R.}_B$, and W_H.

METHODS

Motion picture photographs (16 mm, 128 fps) of swimming and feeding anchovy larvae were used to ascertain the various parameters in the proposed body displacement function $y(x, t) = A(t) \sin\frac{2\pi}{\lambda(t)}(x + \frac{dx_w}{dt}t)$ where $A(t)$ is the wave amplitude of the propagated wave, $\lambda(t)$ the wavelength and $x_w(t)$ the wave position as functions of time. Because of the intermittent character of the motion, variance with x was not considered as important an independent variable as t in the various functions comprising $y(x, t)$. The above displacement function is a general time dependent analogue of the function chosen in Holwill and Miles (1971).

The motion pictures used were obtained from John Hunter of the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, and the techniques used in obtaining them are described fully (Hunter, 1972). The particular sequences used were of fish larvae varying in length from 1.2 to 1.7 cm standard length. All sequences were analyzed starting with the larvae at rest through the sine-wave execution and subsequent forward movement to rest again. The x-axis was considered to be parallel to the direction of forward motion as monitored by a point midway between the eyes of the fish. This point was also used to monitor forward progression.

The sequences were projected with a 16-mm Kodak[2] analyst projector on an elevated stand, through a right-angle mirror onto a table enclosed with a darkened viewing hood. At the beginning of an excursion the contour of the body was outlined with a fine-point pen on heavy-duty, low-absorbance paper. Once the outline was traced, the next frame was advanced (each frame representing $^1/_{128}$ of a second) until the larva came to rest again. The mean excursion time of the larvae examined was 12.9 frames. The contour sequences thus obtained were taken to be representative of the feeding-searching behavior and were used in elucidating the wave-form parameters. In addition to the wave-contour parameters, the midpoint between the eyes was monitored for use in determining Vx and $V'x$.

When the above contours and position points were obtained along with the proper magnification factors derived from knowledge of the lengths of the fish in a particular film, relevant parameter values from the tracings were

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

directly measured using a set of dial calipers read to 0.01 cm.

Many of the initial sequences of an excursion when viewed with respect to the x-axis as defined above showed the appearance of a wave along the proximal portion of the fish while the rest of the body coincided closely to the x-axis. This indicated strong x-dependence of the amplitude in the initial portion of the excursion. However, after three frames an almost symmetrical amplitude wave was observed. Thus the amplitude in the first several frames was taken as the maximum length of the wave above the x-axis (Figure 3).

The wave length was taken as that length between two successive crossings of the x-axis by the displacement wave form. During the later part of the excursions no crossings from positive to negative were observed and at this point the wavelength was taken as twice the value from one tangent of the body on the line of motion to the other (Figure 3).

The position of the midpoint between the eyes after each frame was monitored to yield $x(t)$. Each successive movement of that reference point was recorded in the manner outlined above and the distance moved during each frame noted.

The projected length $x_p(t)$ was taken as the length between the two points representing the projection of the tail and snout tip position on the x-axis and was used in a manner to be described later.

The wave position $x_w(t)$ was taken as the projected length of the body from the point where $A(t)$ is measured to the snout tip (Figure 3).

The points representing the functions described above at each unit of time, i.e., one frame, were collected for 18 excursions which were randomly selected from the larval anchovy feeding films. The functions were then nondimensionalized by division by body length and plotted. The geometric form of the resulting function was then used as a guide in selecting an appropriate descriptive function. The parameters of these functional forms were then fitted by computer in the least squares sense using a nonlinear steepest descent approach (Conway, Glass, Wilcox, 1970). The graphical representation of the proposed body displacement function with the internal functions fitted in this manner was found to coincide very closely with the actual body displacements seen in the films.

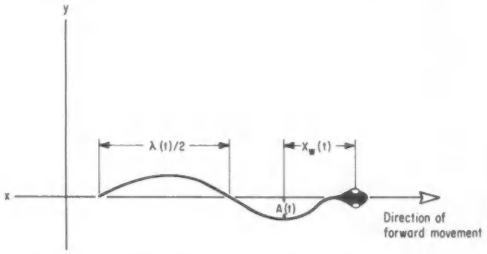

FIGURE 3.—Diagram illustrating the identification of $\lambda(t)/2$, $X_w(t)$ and $A(t)$ from photographic records (see text).

In the derivations for total excursion work, W_T, the integral for tangential viscous reactive work contains s, the distance along the fish body, explicitly. The function satisfying $F(x, t) = s$ is extremely complicated for the complete wave-form displacement function using all the fitted internal functions and is almost impossible to calculate explicitly. The alternative used here is to extrapolate back from the measured $x_p(t)$ to yield $s(x, t)$.

We know the function $F(x, t) = s$ satisfies

$$F(x_p, t) = L$$

where L is the length of the fish body. Since the maximum amplitude ever encountered in this study was around $0.2\,L$ and the mean integration distance never greater than $\pi/2$, we can calculate, for purposes of comparison, the differences between the true length of a pure sine wave of amplitude A and its projected length.

The unperturbed or no sine-wave form for a $\pi/2$ interval of integration yields simply $\pi/2$. The sine-wave projected length is, for $y = A \sin\theta$,

$$s = \int_0^{\pi/2} \sqrt{1 + A^2 \cos^2\theta}\, d\theta$$

$$= \sqrt{1 + A^2}\; E\left(\pi/2, \frac{A}{\sqrt{1 + A^2}}\right)$$

where $E(\Phi, k)$ is the elliptic integral of the second kind (in this case a complete elliptic integral of the second kind). Taking $\lambda \approx 2.0$ cm we get using $A = 0.2L$.

$$s = \sqrt{1 + 0.16}\;\; E(\pi/2, 0.37) = 1.625.$$

The difference between this and $\pi/2$ is about 4%. Thus, we expect the projected length and real body length to differ only slightly. With this confidence we make the following additional assumptions:

$$F(\lambda x_p, t) = \lambda L. \qquad \lambda \leq 1$$

This assumption based on the error calculation above postulates a linear relation between projected length and real length. Now $x_p/L = x_p(t)$ and is obtained from excursion analyses. We can rewrite this as

$$\frac{x_p}{x_p(t)} = L$$

$$\frac{\lambda x_p}{x_p(t)} = \lambda L \qquad \lambda \leq 1$$

$$\frac{x}{x_p(t)} = s \qquad x \leq x_p$$

Thus we chose to identify

$$F(x, t) = x/x_p(t) = s(x, t).$$

The determination of the contour $h(s)$ was made using biologically accurate drawings of a 1.84-cm anchovy larva. The term $h(s)$ was established for the body distal to a vertical line tangent to the gill plate as shown in Figure 4.

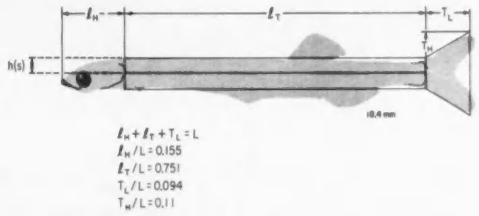

FIGURE 4.—Lateral cross section of 1.84-cm anchovy larvae displaying relationship of idealized contour function $h(s)$ (see text) to appropriate nondimensionalized morphometric parameters.

From that point to the beginning of the tail $h(s)$ was taken as a constant and the relation $h(s) = 0.038\,L$ was found to hold. The dorsal and anal fin contributions were neglected because the plate approximation already constitutes an upper bound estimate for W_T. Thus, the neglect of these fins quantitatively yields a more realistic estimate of W_T. Using the notation of Figure 4 we have,

$$h(s) = 0 \text{ for } s \leq l_H$$

$$h(s) = 0.038\,L \text{ for } l_H < s \leq (l_H + l_T)$$

$$h(s) = 0.038\,L + \frac{(T_H - 0.038\,L)}{T_L}[s - (l_H + l_T)]$$

$$\text{for } (l_H + l_T) < s \leq L$$

or using values in Figure 4 the last relation may be written

$$h(s) = 0.038L + 0.766\,(s - 0.906L).$$

The cross-sectional area A_H which appears in the work integral for the head was determined by randomly selecting Formalin-preserved anchovy larvae from 0.5 to 1.5 cm in length and affixing them, via the Formalin surface tension on their bodies, upright on the side of a small inverted beaker. The largest cross section of the head was then viewed directly with a Nikon optical comparator and an outline traced from the lighted viewing screen. Lengths of the bodies were also measured with dial calipers at the time the tracings were made. Subsequently the tracing areas were measured with a planimeter and corrected to the true value. A least squares analysis of the results yielded the relation $A_H = 0.00423L^{1.23}$ where L is in centimeters and A_H is in square centimeters. The graph is plotted along with the data in Figure 5.

The representation for $\rho(s)$, the linear density of the body, was regarded as constant for any given length and calculated from data in Lasker, et al., (1970). Assuming 90% water, the wet weight of 0.5- to 1.6-cm larvae is then given by $0.00319L^{2.3237} = \rho(s)$ where L is in centimeters and $\rho(s)$ is in grams per centimeter.

The density of the seawater was taken for $T = 17°C$ and was 1.02454. This value was obtained from tables published by the U.S. Navy Hydrographic Office (1956).

In my formulation I assume that the head is propelled through the water as an inert object attached to an undulating body. We want to know the virtual mass and drag coefficient of the inert head for use in the W_H integral. Since the shape of the anchovy larva's head is

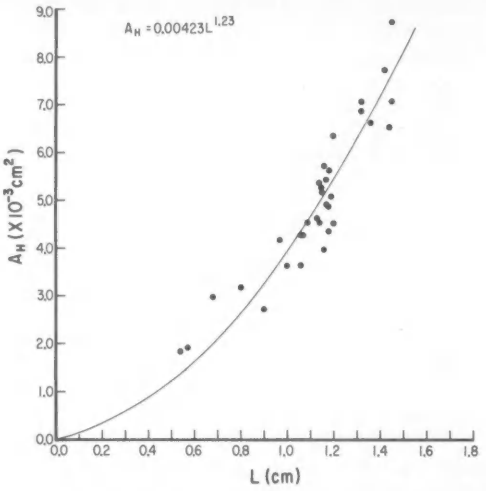

FIGURE 5.—Cross sectional area of larval anchovy head, A_H, as a function of length L.

roughly ellipsoidal or a bluff body, I decided to modify, with due consideration for the geometric differences, the drag relationship observed for a copepod (*Labidocera trispinosa*), which is a naturally occurring bluff body of similar shape, to represent the relevant characteristics of the anchovy larvae head.

If the copepod is taken as an equivalent ellipsoid, we get, from data in Vlymen (1970),

$$\overline{\left(\frac{a_c}{b_c}\right)} = 2.9$$

where a_c is the major axis length and b_c is the semimajor axis length of the copepod *L. trispinosa* and is given respectively by $a_c = \frac{L_c}{2}$ (one-half the metasome length) and $b_c = \left(\frac{A_H}{\pi}\right)^{1/2}$. For the anchovies studied $\frac{l_H}{L} = 0.155$ (Figure 4) and for $\bar{L} = 1.4$ cm and $A_H = 0.007$ cm^2, $l_H = 0.217$ cm yielding $\overline{\left(\frac{a_a}{b_a}\right)} = 2.3$.

For high Reynolds numbers ($\sim 10^4 - 10^5$) and rotationally symmetrical bluff bodies of various l/d ratios, where l is the bluff body length and d is diameter, we have

$$\frac{C_D}{C_f} = 3\left(\frac{l}{d}\right) + 4.5\left(\frac{d}{l}\right)^{1/2} + 21\left(\frac{d}{l}\right)^2$$

(Hoerner, 1965)

where C_f is the frictional drag coefficient based on wetted surface area and C_D. is the drag coefficient based on frontal area. We can use this relation to approximate $\frac{C_D.\ (\bar{l}/d = 2.9)}{C_D.\ (\bar{l}/d = 2.3)}$ assuming $C_f(l/d = 2.9) \cong C_f(l/d = 2.3)$, and use the above ratio to modify the measured drag relation already obtained for the copepod. Substituting $l/d = 2.9$ and $l/d = 2.3$ into the relation for $C_D./C_f$ we get on dividing

$$\frac{C_D \cdot\ (l/d = 2.9)}{C_D \cdot\ (l/d = 2.3)} = 1.00.$$

At lower Reynolds numbers we expect the geometric differences to cause a greater discrepancy between $C_D.\ (l/d = 2.9)$ and $C_D.\ (l/d = 2.3)$. In particular $C_D.\ (l/d = 2.9) > C_D\,(l/d = 2.3)$. However, since in my experiments Re was from 0- to 100, the region where we expect the $C_D\,(Re)$ curve to flatten out to a fairly constant value we take $C_D\,(Re)$ for the copepod as a first approximation to the $C_D.\,(Re)$ for the anchovy head. That function is $C_D\,(Re) = 85.2/Re^{.80}$, Vlymen (1970). The virtual mass, m, occurring in the integrals for W_H is then calculated by considering the head as if it were an equivalent ellipsoid. Using $(a_a/b_a) = 2.3$ we can calculate

m as $m = k_1 \rho V_D$ where $k_1 = \frac{\gamma}{(2 - \gamma)}$

$$\gamma = 2\left(\frac{1-\epsilon^2}{\epsilon^3}\right)\left[1/2 \log\left(\frac{1+\epsilon}{1-\epsilon}\right) - \epsilon\right]$$

$$\epsilon = \left(1 - \frac{b_a^2}{a_a^2}\right)^{1/2}$$

$V_D = 4/3\,\pi a_a b_a{}^2$ Vlymen (1970).

For a 1.4-cm larva m has a value of 1.80×10^{-4} g and assuming the head density is the same as seawater we get $M = 7.9 \times 10^{-4}$ g. Thus W_H may be rewritten as

$$W_H = 1/2 \int_0^{t_E} 85.2\left(\frac{\nu}{L}\right)^{.80} V_x{}^{2.2} A_H\, dt$$

$$+ \int_0^{t_E} (9.7 \times 10^{-4} \frac{dV_x}{dt} V_x\, dt$$

where ν is the kinematic viscosity of seawater 0.0119 cm^2-s^{-1} (U.S. Navy Hydrographic Office, 1956).

A computer program by Stroud (1971) using 16-point Gauss-Legendre integration, and the above outlined integration scheme was used to compute the integrals comprising W_T. The program was translated into Algol and executed on a Burroughs 6700 at the University of California, San Diego Computer Center. Accuracy of the program was checked by evaluation of the iterated integrals

$$\int_0^w e^{-y^2}\,dy \int_0^x e^{x^2}\,dx \text{ for various } w \text{ and}$$

$$\int_0^1 \int^{\sqrt{1-x^2}} \sqrt{1-x^2-y^2}\,dy\,dx = \frac{\pi}{6}.$$

The results showed the integration scheme to be accurate to the eighth decimal place in the former integral when compared with tables in Rosser (1948) and accurate to the fourth decimal place in the latter integral using standard tables. Details of the mathematical scheme are found in the appendix.

In the integrations of W_T a relative convergence was computed by first doing the integration over the whole interval, that is,

$$I_0 = \int_0^t \int_{f(t)}^{g(t)} F(x, t)\,dxdt.$$

Then the value corresponding to one subdivision is computed, namely,

$$I_1 = \int_0^{t/2} \int_{f(t)}^{g(t)} F(x, t)\,dxdt + \int_{t/2}^{t} \int_{f(t)}^{g(t)} F(x, t)\,dxdt.$$

The relative convergence is then computed as

$$C = \frac{I_1 - I_0}{I_1}.$$

If this value is less than 0.05, the value I_2 is taken as the value of the integral. If it is greater, the intervals comprising I_2 are further subdivided and the process continued until convergence is reached. Thus, if I_n, corresponding to 2^n subdivisions, and I_{n+1}, corresponding to 2_{n+1} subdivisions, are of such values that

$$\frac{I_{n+1} - I_n}{I_{n+2}} < 0.05,$$

then I_0 is assigned the value I_{n+1}.

The convergence is set higher than one might expect because computation of the complex integrals of the type used in this study is manifested by slow and oscillatory relative convergences necessitating a great deal of computer time. However, when the convergence criteria was set at 0.05 in the integrations performed, convergences were better than the critical value. The effect of the higher convergence criteria is thus seen as being an economic and computational convenience.

RESULTS

The plotted values of the nondimensional amplitude, $A(t)/L$, wave position, $X_w(t)/L$, and projected length, $X_p(t)/L$, along with the descriptive functions fitted by the methods discussed are shown in Figures 6 and 7. The points comprising the curves of each represent the mean value of the particular parameter in question at successive units of time where one time unit is $^1/_{128}$ s.

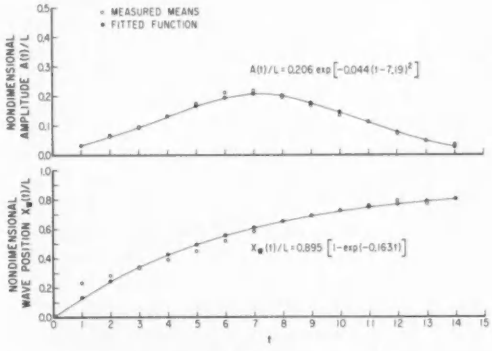

FIGURE 6.—Nondimensional amplitude, $A(t)/L$ and wave position, $X_w(t)/L$, of body displacement function as functions of time, t, in motion frame units. The graphs display the fitted curves (line) together with the original data (open circles) and points of the fitted curve at corresponding time units (closed circles).

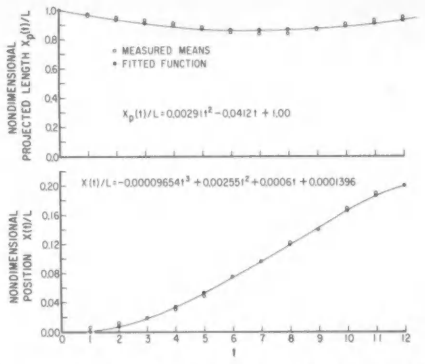

FIGURE 7.—Nondimensional position, $X(t)/L$, and projected body length, $X_p(t)/L$, as functions of time, t, in motion frame units. The graphs display the fitted curves (lines) together with the original data (open circles) and points of the fitted curve at corresponding time units (closed circles).

The curve for $\lambda(t)/L$, deserves some discussion. Since the amplitude of the propagated wave was known to be zero at $t = 0$, both $\lambda = \infty$ or $\lambda = 0$ would be descriptive of the initial straight-line configuration. However, $\lambda = 0$ implies an infinite number of oscillations varying like sin t/λ with neither the function nor the first derivative existing as $\lambda \rightarrow 0$. Since at the end points of an excursion a slightly perturbed wave form was observed, i.e., a finite wavelength, the nondimensional wavelength of the $t = 0$ excursion wave form was adjusted to be equal to the last. A perfect relation

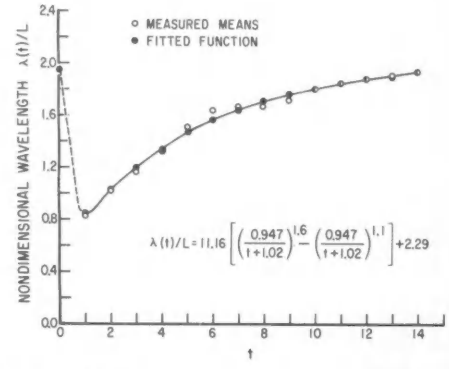

FIGURE 8.—Nondimensional wavelength, $\lambda(t)/L$, as a function of time, t, in motion frame units. The graph displays the fitted function (line) together with the original data (open circles) and points of the fitted curve at corresponding time units (closed circles). The dotted portion of the fitted curve is discussed in the text.

would have $\lambda = \infty$ at both end points. This, I believe, does not drastically affect the results since the only modulatory component at the end points is the amplitude which is zero at these points. This accounts for the Lennard-Jones type of function which was chosen as a functional representation of $\lambda(t)/L$ and is shown in Figure 8 along with the function itself. The values at other than the end points together with the fact that $A(t) = 0$ at these points is sufficiently descriptive of the contour wavelength to vitiate any physical inconsistencies or mathematical problems that may arise from the end point modification of $\lambda(t)/L$ discussed.

The integrals representing the work per excursion namely $W_B^{V.R.}$, W_B^A, W_H were subdivided further into smaller iterated integrals and, using the mean excursion time of 12.9 frame time units (~0.10s) integrated by the method already outlined. The values obtained were taken to represent the work/excursion of an anchovy larvae of length equal to the mean of the animals used in the study or 1.4 cm.

The values of the work are divided into five categories as follows: 1) head energy representing the value of the integral in Equation (3), 2) normal energy representing the value of the 1st integral of $W_B^{V.R.}$, 3) tangential energy representing 2nd integral of $W_B^{V.R.}$, 4) body inertial energy representing the 1st integral of W_B^A, and 5) inertial energy representing the 2nd integral of W_B^A. The value of these five integrals in ergs/excursion and their fraction of the total excursion energy is given in Table 1. It is observed from the table that accelerative terms such as body inertial and inertial energies account for more than three-fourths of all the energy used in swimming. It is worthwhile noting that although this is an expected outcome of the peculiar behavior of the anchovy larvae, it is possibly true that neglect of such terms in many analyses of fish energetics is cause for errors. Attention to these matters has been given thorough theoretical discussion in Lighthill (1970, 1971). The analysis in this paper,

TABLE 1.—Excursion energy components in ergs for the 1.4-cm anchovy larva.

Item	Energy/ excursion	Percent of total
Normal energy	11.5	7.9
Tangential energy	0.35	0.2
Inertial energy	33.6	23.2
Body inertial energy	99.2	68.5
Head energy	0.15	0.2
Total energy	144.8	

however, depends on incorporating what actually occurs into an easily manipulated theoretical energy construct.

Although the point of this study is to evaluate the swimming energetics in an indirect but nonmanometric manner, it is nevertheless interesting to compare the calculated energy using the theoretical model with values obtained using O_2 consumption measurements obtained with anchovy larvae. Such experiments in limited numbers have been performed by Lasker (pers. commun.) using more than one larva per experiment and with the animals confined to small volume containers. No knowledge of activity levels was possible during these experiments and the values obtained reflect total O_2 uptake per experimental period averaged for the number of larvae per container. Lasker believes, however, that activity levels during such experiments are below natural levels because of the inhibiting effects of the container surfaces and crowding. The value obtained from such experiments was 4.36 ± 1.05 μl O_2/mg dry wt/h. Assuming an RQ of 0.70 we get 1 μl O_2 = 0.005 cal ± 0.00035 (Lasker, 1962). Thus, the caloric equivalent of the anchovy larval respiratory rate is between 0.0153 cal/mg dry wt/h and 0.0289 cal/mg dry wt/h with a mean value of 0.0218 cal/mg/h (n = 23). A comparison between the theoretically determined energy value and the mean O_2 uptake value given above requires a simultaneous knowledge of swimming activity expressed as an excursion frequency. Such information is not available and it is precisely our inability to make simultaneous observations of O_2 consumption and activity of fish larvae that necessitates the type of study undertaken in this paper. Excursion rates observed during 5-min feeding-searching periods have been measured (Hunter, 1972) using large containers. For the periods observed the excursion rate appropriate to a 1.4-cm larvae was found to be 1.57 ± 0.03 excursions/s with the mean time devoted to intermittent swimming being 82.6% ± 1.2%. This value is probably a maximum for activity since satiation would probably lead to a decrease in excursions as would the lack of observable food particles. Since available O_2 measurements were not collected during feeding, some modification of the above activity value has to be made to compensate for the inhibition of the container and the absence of food before these values can be used for comparison.

The O_2 consumption measurements of anchovy larvae were performed in small 70-ml containers in light and darkness. The only relative activity measurements that have been performed for similar situations were on 28-day-old herring larvae ca. 1 cm in length in a variety of light conditions by Blaxter (1973). Although herring are continuous swimmers, unlike anchovy larvae, the use of relative activities was deemed an appropriate way of estimating the activity variation of a similar sized nonfeeding organism in the following manner. For herring larvae at 10 different light levels the mean percent difference between maximum and mimimum activity levels was found by Blaxter (1973) to be 78.6%, maximum activity being defined as mean activity plus two standard errors and minimum activity as mean activity minus two standard errors. Although this change is large, it probably reflects behavioral modulation more than effects of the container since in Blaxter's experiment the container (a long tube) contained approximately 1,500 ml of seawater. Thus, regarding the O_2 consumption experiments on the anchovy as representing the minimum activity levels of that organism in the same relationship of active to inactive as found from Blaxter (1973), we can, using known maximum excursion rates during feeding from Hunter (1972), calculate the minimum excursion rate or activity corresponding to our O_2 measurements and hence the energy consumption for swimming based on that excursion rate. This analysis assumes the geometric swimming behavior during feeding and nonfeeding is the same, an assumption confirmed by observation.

Using the mean O_2 consumption value 0.0218 cal/mg dry wt/h and the dry weight of a 1.4-cm larva from Lasker et al. (1970) we get an expenditure of 22.6×10^{-3} cal/h. Taking 1.57 excursions/s as the mean maximum activity value, decreased by 78.6% to convert to minimum activity levels, and multiplied by the theoretically determined energy per excursion of the 1.4-cm larva of 144.8 ergs/excursion, we get 4.91×10^{-3} cal/h. This value yields an estimate of metabolic swimming efficiency of 24.6% for the 1.4-cm larval anchovy assuming a poikilothermic basal metabolic rate of 0.05 μl O_2/mg wet wt/h. This efficiency is quite high when compared to values obtained for larger fish where efficiencies in the range of 8 to 15% (Webb, 1971) are observed. However, such experiments are usually done on large fish constrained by relatively small tanks, swimming continuously, and using a caudal propeller mode of propulsion. Thus any comparison of the above results

with the wide-range Reynolds number motions and large amplitude wave forms encountered in this study must be done cautiously and with appropriate consideration of hydrodynamical dissimilarities. However, using the most obvious behavioral differences between the two types of studies, a higher overall efficiency might be suspected based on the viewpoint of Lighthill (1971) that the large amplitude tail motions exhibited by some fishes be interpreted as a means of producing reactive thrusts which balance the enhanced viscous drag produced upon the commencement of lateral movements. Lighthill thus implies that large amplitude movements interspersed with periods of gliding are more efficient than continuous small amplitude oscillations as a mode of propulsion. This appears to be confirmed in the results of this study where the behavior is of this type and the efficiency apparently high. It should be stressed that a range of efficiencies can exist due to the intrinsic variability in O_2 consumption values and associated activity measurements and the fact that synchronous determinations of both have not yet been performed. The purpose of the swimming efficiency calculation and the associated comparison curves with O_2 values (Figure 9) is to demonstrate the relationship the theoretical values determined here have to the available physiological parameters obtained with simple experimental designs. If excursion energies could be obtained by simpler means, one could circumvent the involved procedures presented in this paper.

It is interesting to note that the Pacific sardine, *Sardinops caerulea*, whose ecological niche was primarily taken over by the anchovy, *Engraulis mordax*, in the California Current (Murphy, 1966) does not exhibit, in the larval stages, the same swimming behavior as the anchovy, i.e., swimming bursts followed by glides. Instead it swims by constant, small amplitude oscillating movements of the body. In light of the results here and theoretical work by Lighthill it is possible that the propulsive efficiencies in the larval stages of the sardine and anchovy are slightly different, the sardine being less efficient. Thus a small behavioral-propulsive difference between the anchovy and the sardine might have permitted the anchovy to compete more favorably when there was a decline in sardine population.

The evaluation of propulsive energetics as outlined in this study is directed at only one size of the anchovy larva because the method

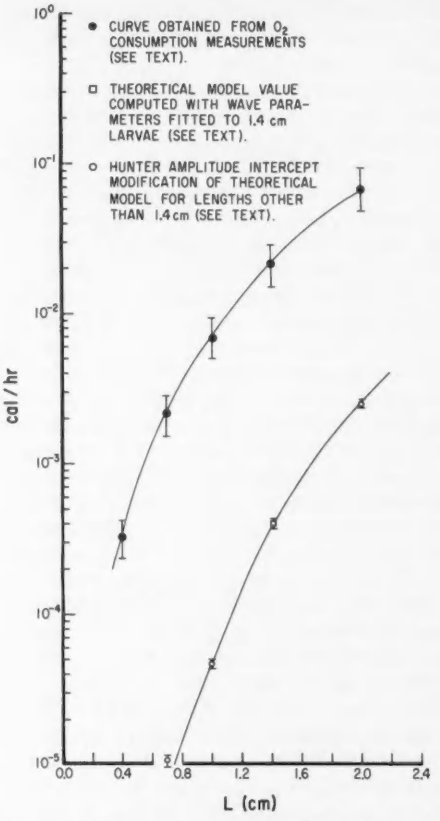

FIGURE 9.—Energy consumption of swimming based on theoretical model (open circles and open square) and total energy consumption based on O_2 utilization (closed circles) as a function of length. Vertical lines on both curves span one standard error of the data.

requires detailed knowledge of the various wave-form parameters as functions of time for each length of the organism studied. Valid results cannot be obtained for other sizes by a mere alteration of the length of the organism in the wave-parameter functions. By the method outlined here, the only way to properly evaluate propulsive energetic costs for different lengths would be to repeat the course of wave-parameter determination completely. However, with such limitations in mind it is interesting to compare results obtained when modification of the existing wave-parameter functions is made using extensions of known length-dependent wave-parameter quantities which have been measured for larval anchovies. The

only such wave parameter available for modification and incorporation into the energy formulation is the wave amplitude.

Hunter (1972) measured the relationship between tail-beat amplitude and larval length for intermittent swimming and found the relationship,

$$A = 0.112 + 0.170L$$

where L and A are in centimeters. Since minimal amplitude dependence on length exists because of the exaggerated whiplike motion of the tail, Hunter's amplitude value is greater than my value for the maximum wave amplitude of 1.4-cm larvae. This is because amplitudes used in this study are measured as the wave crest progresses caudally at each successive time unit, whereas at the tail, wave progression ceases along the body and may even become retrograde due to the whiplike motion. The important point is the intercept at zero length where both measurements must be consistent, i.e., equal. Thus, admitting equality of the interception point at $L = 0$ and adjusting the first order coefficient in Hunter's equation to yield the correct value for maximum amplitudes at L = 1.4 cm we get,

$$A_{\max} = 0.112 + 0.094\ L$$

This value was substituted for $A_{\max} = 0.026\ L$ in the amplitude function $A(t) = 0.206\ L \exp[-0.044\ (t - 7.19)^2]$ and its first two derivatives used in the L = 1.4 cm formulation. The work integrals were then recomputed at the three new points L = 0.4 cm, L = 0.7 cm, and L = 2.0 cm. Because the $A_{\max}$ values coincided at L = 1.4 for both treatments this value was not used again in the integration procedure. The values obtained are shown in Table 2. Least squares regression of the data assuming the functional form $E = aL^b$ where E is energy/excursion in ergs and L length in centimeters yielded $E = 27.5\ L^{4.48}$. The energy/excursion calculated for the four additional lengths was then converted to hourly energy rates using the excursion frequencies cited earlier. The results obtained were plotted with scales of calories per hour vs. length in centimeters. For comparison, another curve of the form $\frac{dO_2}{dt} = f(L)$ was computed and plotted along with the curve formed using the additional model points above (Figure 9). The line shown connecting these points is fitted by eye. The comparison curve was based on the respiration value of 0.0218 cal/mg dry wt/h and the following relationship between dry weight in milligrams and length in millimeters, $\log W = 3.3237 \log L - 3.8205$ (Lasker et al., 1971). This comparison curve is isomorphic to the length-weight curve with no allowance being made for specific respiration changes with increasing weight. Therefore the curve is to be regarded as the best approximation to the total O_2 consumption rate for swimming larval anchovies. It provides only a means of judging the physiological reliability of the energy summation method employed here. However, because the changes in specific respiration as a function of weight would not change this comparison curve appreciably, it can probably be regarded as sufficiently reliable. With this understanding some comparison of these curves can be made.

TABLE 2.—Excursion energies for five larval anchovy lengths using Hunter's modified intercept amplitude function (see text for complete discussion) for extension to larval lengths other than 1.4 cm.

Length (cm)	Energy/ excursion (ergs)
2.0	881.4
1.4	144.8
1.0	16.3
0.70	3.6
0.40	0.76

From laboratory observation of larvae it seems apparent that nondimensional amplitude and wavelength do not remain constant but decrease in absolute value as length is increased. That is, functions descriptive of these nondimensional parameters do not remain descriptive of animals of all lengths. That is exactly what is observed as we deviate from the original L = 1.4 cm point where the nondimensional wave parameters are fitted. Even with modification of $A_{\max}$ used to compute the original curve this effect is still observable. Part of the deviation is, however, due to the behavior of the larvae as age increases. Very small larvae float 90% of the time with occasional bursts of intensive activity (Hunter, 1972) which, as I pointed out earlier, is quite inefficient. As the larvae get older, however, intermittent, more efficient swimming becomes the dominant mode of locomotion. This trend is partially reflected in these two curves. As the larvae get older and

larger the intermittent swimming rate decreases and the nondimensional amplitude and wave functions decrease also. This accounts for the large locomotion energy computed for larvae greater than 1.4-cm in length. It is interesting to note how behavioral factors, when unavoidably neglected in extending this curve, become evident when compared with reasonable estimates for total energy consumption.

In view of the behavioral-mathematical factors influencing the shape of the theoretical curve in the directions observed here and the physiologic reasonableness of the metabolic swimming efficiencies obtained when exact wave parameters descriptive of the L = 1.4-cm larva are used, it is reasonable to conclude that the energies calculated from the model are the best estimates of the swimming energetic requirement per excursion of the larval anchovy, excursion being regarded as a discrete, reproducible behavioral entity, currently available.

Therefore, the major results of this study are 1) the demonstration that modifications of existing methods of computing energy of translation yield information on behavior when consideration is given to differences in behavior, shape, and flow scale, 2) that a good correlation exists in terms of metabolic swimming efficiency obtained between direct O_2 measurements and the model, 3) a confirmation of the high efficiency of large amplitude, intermittent swimming behavior, and 4) quantitative estimates of swimming energy requirements derived from this model may be used for other larval anchovy research.

Theoretical studies such as random walk analyses and correlations with feeding behavior and migration which are being studied currently could incorporate these data to provide a comprehensive and quantitative picture of larval anchovy energetics and behavior.

ACKNOWLEDGMENTS

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APPENDIX

The integration of the iterated integrals was accomplished via a two-dimensional extension of the standard Gauss-Legendre guadrature. The one-dimensional fixed limit integration formula was used by Holwell and Miles (1971) for similar classes of functions with good results. The type of integrals requiring evaluation were of the general form

$$\int_a^b \int_{f(t)}^{g(t)} F(x, t)\, dxdt$$

a, b, fixed.

Defining

$$G(t) = \int_{f(t)}^{g(t)} F(x, t)\, dx,$$

we get

$$\int_a^b \int_{f(t)}^{g(t)} F(x, t)\, dxdt = \int_a^b G(t)dt.$$

By n-point Gauss-Legendre quadrature Abramovitz and Stegun (1966) this is given approximately by,

$$\int_a^b G(t)dt \cong \frac{b-a}{2} \sum_{i=1}^{n} w_i\, G(\xi_i)$$

where $\xi_i = \frac{b-a}{2}\, y_i + \frac{b+a}{2}$

$y_i = i$th zero of $P_n(x)$, the n-order Legendre polynomial and

$$w_i = 2/\left(1 - y_i^2\right)\left[P'_n(\xi_i)\right]^2 .$$

Using Gauss-Legendre quadrature on $G(\xi_i)$ yields,

$$\int_a^b G(t)dt \cong \frac{b-a}{2} \sum_{i=1}^{n} w_i \int_{f(\xi_i)}^{g(\xi_i)} F(x, \xi_i)\, dx$$

$$\cong \frac{b-a}{2} \sum_{i=1}^{n} w_i \frac{g(\xi_i) - f(\xi_i)}{2} \sum_{j=1}^{n} w_j^* F(\eta_j, \xi_i),$$

where $\eta_j = \frac{g(\xi_i) - f(\xi_i)}{2}\, y_j + \frac{g(\xi_i) + f(\xi_i)}{2}$

$w_j^* = 2/(1 - y_j)\left[P'_n(\eta_j)\right]^2$ and

$y_j = j$th root of $P_n(x)$.

We have finally the result,

$$\int_a^b \int_{f(t)}^{g(t)} F(x, t)\, dxdt \cong \frac{b-a}{2} \sum_{i=1}^{n}$$

$$\sum_{j=1}^{n} w_i\, w_j^* \frac{g(\xi_i) - f(\xi_i)}{2} F(\eta_j, \xi_i),$$

where the above definitions hold.

ANALYSIS OF MIGRATIONS AND MORTALITY OF BLUEFIN TUNA, *THUNNUS THYNNUS*, TAGGED IN THE NORTHWESTERN ATLANTIC OCEAN[1,2]

F. J. MATHER III,[3] B. J. ROTHSCHILD,[4] G. J. PAULIK,[5] AND W. H. LENARZ[4]

ABSTRACT

An analysis is presented on the release and return data from bluefin tuna, *Thunnus thynnus*, tagged in the northwest Atlantic Ocean from 1954 to 1970. There was an apparent northward movement of fish from the New Jersey area as the fishing seasons progressed. Tag returns from bluefin released in the Long Island and southern New England areas tended to be to the north at first and then to the south. Mean distances between release and return tended to be greater for fish released in the New Jersey area than for the other two areas. Estimates of mortality rates for tagged bluefin were made using the Chapman-Robson method and then adjusted for Type-I and Type-II tag shedding and Type-I tagging mortality. The average estimate of instantaneous fishing mortality is 0.57 and other losses (natural, tagging, and emigration) is 0.68 on an annual basis. The estimate of other losses is considerably higher than the natural mortality that would be expected for bluefin. Evidence is presented suggesting that the rate of emigration may be quite high. The average single season exploitation rate of tagged bluefin was estimated to be 0.33. It was noted that since bluefin may be both immigrating to and emigrating from the fishery the estimate of exploitation may not be representative of the entire population. Even though validity of available effort data is questionable, regression estimates of mortality and survival rates were made using catch per effort data. These estimates of survival are lower than those obtained using the Chapman-Robson method.

The data which form the basis for this report were assembled by the first author. This study is based upon releases of tagged bluefin tuna, *Thunnus thynnus*, that were made by a variety of organizations and individuals under the coordination of the Woods Hole Oceanographic Institution Cooperative Game Fish Tagging Program at various locations along the middle Atlantic bight of North America from July 1954 to August 1970 and returns of these tags to the end of 1970. Additional returns are expected in the future from more recent releases.

MIGRATIONS

Because of the variety of methods, locations, and dates of release, we needed to assemble the data by relatively homogeneous release groups. The criterion for constructing a release group for analysis of migrations was to develop homogeneous time-location strata of releases from which a minimum of 20 tags were recovered. This procedure allowed us to work with homogeneous groups, but eliminated roughly 10% of the recovered tags from our analysis. Table 1 summarizes these release groups and Figure 1 shows their localities. We can see from Table 1 that during the study period the tagging operations tended to shift from the New Jersey coast, to the New York coast, to the southern New England coast, and that releases in July tended to be south of those made in August or September.

Tagging data have been used to show some of the longer migrations of the bluefin tuna (Food and Agriculture Organization, 1972). We examined the shorter term recoveries from an analytic point of view. In order to do this, we made use of a method developed by Rothschild (Bayliff and Rothschild, in press). Using this method each release group was stratified into intervals of time at liberty. Release vectors (latitude and longitude) for each release group were used to compute an average or common release vector. Each recapture vector for the group was then standardized to the common release vector. The standardized vectors were then used to find 1) the average recapture vector and 2) the determinant of the recapture

[1]This paper is dedicated to the memory of Gerald J. Paulik. He was a good friend and colleague and made important contributions to the theory of tagging.

[2]Contribution No. 3180, Woods Hole Oceanographic Institution, Woods Hole, MA 02543.

[3]Woods Hole Oceanographic Institution, Woods Hole, MA 02543.

[4]Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92037.

[5]College of Fisheries, University of Washington, Seattle, WA 98195. Deceased.

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TABLE 1.—Release groups used for analysis of migrations of tagged bluefin tuna.

	General location of release					
	New Jersey Coast		Long Island Coast		Southern New England	
Release date	Group No.	No. of returns	Group No.	No. of returns	Group No.	No. of returns
July 1964	2A	33				
	2B	32				
	2C	27				
Aug. 1964			3	33		
July 1965	4A	36				
	4B	56				
	4C	38				
Aug. 1965	5A	22	5B	47	5C	24
July 1966	6A	114				
	6B	127				
	6C	45				
	6D	85	6E	62		
Aug. 1966			7A	20	7C	85
			7B	81	7D	36
					7E	55
					7F	203
					7G	177
Sept.-Oct. 1966			8	23		
July 1967	9A	23				
	9B	94				
Sept. 1967			10	27		
July 1968	11A	21	11B	39		
July 1969			12	24		
Aug. 1969					13	40
Sept. 1969					14	22
July 1970					15	17
Aug. 1970					16	25
1954-63					17	24

variance-covariance matrix. The determinant of the recapture variance-covariance matrix is proposed by Bayliff and Rothschild as an index of the dispersal of the fish. When the distance of the recoveries from one another is large, the determinant is large.

It should be noted that the vectors computed by this method are not on a per-unit-effort basis so that "migration patterns" reflect not only the apparent movement of the fish, but also the distribution of fishing effort. In order to more fully understand the nature of short-term movements, it will be necessary to study in some detail the complex problem of the distribution of bluefin tuna in the northwest Atlantic. Preliminary to more detailed analysis of these statistics, we surveyed some of the main features of the data, of which some are tabulated in Table 2.

First we considered the direction of movement. Figure 2 contains a synthesis of these data and shows the direction of movement by tagging location and time at liberty. It is implicit that we treated each symbol as reflecting the behavior of a sample of fish from the same statistical population. The main features of Figure 2 are that fish tagged off New Jersey in July tended to move in an eastward direction and both north and south during the first 2 wk at liberty, but then movement became strongly directed to the northeast. Fish released in the Long Island area initially tended to move toward the north, but after the first 30 days, their movement appeared to have been concentrated to the west and south. The same conclusion may be obtained from the southern New England releases.

An examination of the mean distance (Figure 2) shows fish released off New Jersey tended to be recovered at a slightly greater distance to the north than the south. The fish moved approximately 7 or 8 miles per day. By the second 15-day period, the fish moved about 60-100 miles to the northeast. The pattern for Long Island releases, based on only a few observations, shows that movement distance of these fish during 1-15 days was approximately the same as that for the New Jersey releases. The short-term recoveries of southern New England tagged fish reflect even less average distances than New Jersey short-term releases suggesting that either the fish off southern New England moved less than off New

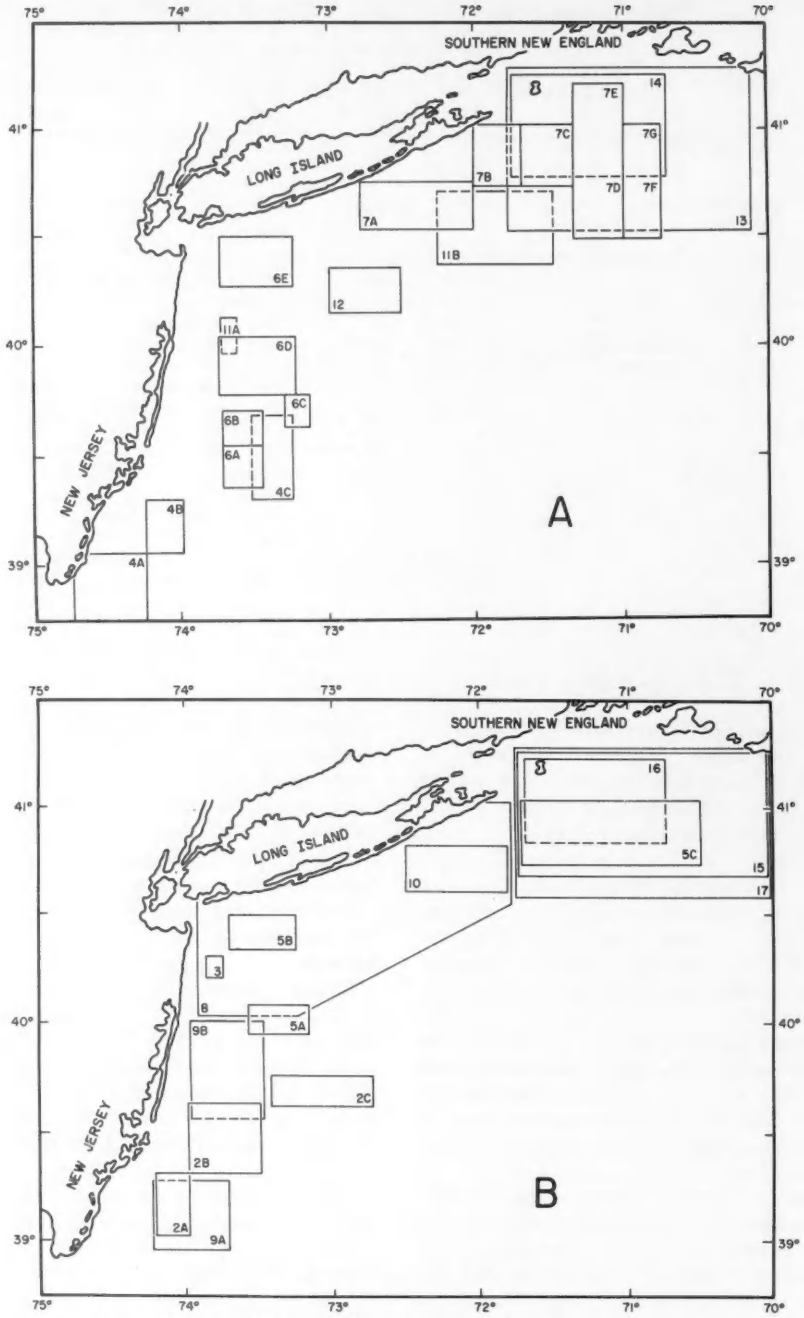

FIGURE 1.—Part A and Part B: Map of middle Atlantic bight showing release group locations of tagged bluefin tuna.

TABLE 2.—Summary of statistics on movements of tagged bluefin tuna. All distance measures are nautical miles.

Release group	Time at liberty (days)	Mean miles N-S[1]	Mean miles E-W[2]	Determinant (x 10^4)	Mean distance	No. of fish	Release month	General release location
2A	1-15	26.5	34.1	2.3	50.5	13	July	N.J.[3]
	16-30	74.2	74.9	26.0	114.0	9	1964	
	31-60					1		
	61-180					0		
2B	1-15	−9.2	11.4	2.9	31.8	18	July	N.J.
	16-30	25.1	58.5	1.4	89.7	7	1964	
	31-60					2		
	61-180					0		
2C	1-15	−7.2	−15.0	1.3	29.6	14	July	N.J.
	16-30					1	1964	
	31-60					1		
	61-180					0		
3	1-15	8.0	12.2	0.3	32.6	12	Aug.	L.I.[4]
	16-30					1	1965	
	31-60					0		
	61-180					0		
4A	1-15	12.0	18.3	3.8	33.6	18	July	N.J.
	16-30	83.6	52.8	11.7	102.0	8	1965	
	31-60					1		
	61-180					1		
4B	1-15	20.9	7.4	8.7	46.4	39		N.J.
	16-30	70.8	21.2	0.2	74.6	28		
	31-60					3		
	61-180					0		
4C	1-15	25.3	−16.6	13.4	47.9	17	July	N.J.
	16-30	62.3	3.1	1.1	64.8	13	1965	
	31-60					0		
	61-180					0		
5A	1-15	25.8	−15.4	19.4	48.5	9	Aug.	N.J.
	16-30	53.5	5.4	17.2	60.4	12	1965	
	31-60					0		
	61-180					0		
5B	1-15	24.8	−17.9	9.5	47.2	8	Aug.	L.I.
	16-30	44.8	−1.8	36.0	54.9	5	1965	
	31-60					0		
	61-180					0		
5C	1-15					0	Aug.	S.N.E.[5]
	16-30					0	1965	
	31-60					0		
	61-180					0		
6A	1-15					2	July	N.J.
	16-30					3	1966	
	31-60	59.1	25.9	18.7	86.4	11		
	61-180	57.0	−11.1	0.01	58.6	23		
6B	1-15					4	July	N.J.
	16-30	52.8	39.6	0.2	76.7	5	1966	
	31-60	62.2	70.0	90.9	112.0	20		
	61-180					4		
6C	1-15					0	July	N.J.
	16-30					2	1966	
	31-60					1		
	61-180	39.9	−23.7	0.002	46.7	9		
6D	1-15	−5.5	5.6	62.3	41.1	10	July	N.J.
	16-30	4.0	3.3	1.7	20.7	6	1966	
	31-60	30.6	15.6	51.9	64.7	9		
	61-180	30.0	−13.2	0.006	33.1	14		

See footnotes at end of table.

TABLE 2.—Continued.

Release group	Time at liberty (days)	Mean miles N-S[1]	Mean miles E-W[2]	Determinant (x10[4])	Mean distance	No. of fish	Release month	General release location
6E	1-15	−28.2	3.0	1.8	35.9	14	July	L.I.
	16-30	5.0	58.1	36.0	82.4	6	1966	
	31-60					3		
	61-180	−3.8	−3.6	1.2	16.8	10		
7A	1-15					1	Aug.	L.I.
	16-30					2	1966	
	31-60					1		
	61-180					0		
7B	1-15	0.6	22.1	0.8	26.8	11	Aug.	L.I.
	16-30	−11.4	−15.5	8.8	52.4	7	1966	
	31-60					1		
	61-180					0		
7C	1-15	−2.0	6.0	1.3	17.9	9	Aug.	S.N.E.
	16-30	−3.6	6.0	1.0	28.9	8	1966	
	31-60					1		
	61-180					0		
7D	1-15	13.2	2.5	6.2	28.2	10	Aug.	S.N.E.
	16-30	7.2	−14.9	12.0	46.5	8	1966	
	31-60					1		
	61-180					0		
7E	1-15	−17.3	2.6	8.8	29.3	15	Aug.	S.N.E.
	16-30	−8.8	−21.7	30.3	50.3	5	1966	
	31-60					1		
	61-180					0		
7F	1-15	7.5	−20.0	4.5	36.0	39	Aug.	S.N.E.
	16-30	7.5	−17.4	3.3	28.9	65	1966	
	31-60	1.3	−26.2	15.6	48.0	14		
	61-180					1		
7G	1-15	−3.8	−19.1	3.0	32.2	37	Aug.	S.N.E.
	16-30	−0.7	−15.9	3.1	29.9	50	1966	
	31-60	−4.6	−24.6	12.8	48.0	14		
	61-180					1		
8	1-15					1	Sept.-	L.I.
	16-30					0	Oct.	
	31-60					0	1966	
	61-180					0		
9A	1-15					2	July	N.J.
	16-30	87.7	12.7	0.003	69.1	9	1967	
	31-60	86.8	26.8	9.4	76.6	8		
	61-180					0		
9B	1-15	−18.4	−7.1	1.0	27.4	14	July	N.J.
	16-30	13.1	−3.6	1.7	24.0	12	1967	
	31-60	27.0	7.1	13.5	39.3	47		
	61-180					2		
10	1-15					0	Sept.	L.I.
	16-30					0	1967	
	31-60					2		
	61-180					0		
11A	1-15					0	July	N.J.
	16-30					2	1968	
	31-60					0		
	61-180		−4.0	0.008	22.8	9		
11B	1-15	5.8	22.4	4.2	32.8	13	July	L.I.
	16-30	10.4	35.8	0.3	39.9	11	1968	
	31-60					1		
	61-180					4		
12	1-15					4	July	L.I.
	16-30					0	1969	
	31-60					4		
	61-180					0		

See footnotes at end of table.

TABLE 2.—Continued

Release group	Time at liberty (days)	Mean miles N-S[1]	Mean miles E-W[2]	Determinant ($\times 10^4$)	Mean distance	No. of fish	Release month	General release location
13	1-15					1	Aug.	S.N.E.
	16-30					1	1969	
	31-60					1		
	61-180					0		
14	1-15					0	Sept.	S.N.E.
	16-30					0	1969	
	31-60					0		
	61-180					0		
15	1-15					3	July	S.N.E.
	16-30	−1.7	−20.6	3.5	28.1	9	1970	
	31-60	−24.4	−6.8	0.5	28.2	5		
	61-180					0		
16	1-15	−13.1	−14.7	2.0	28.3	9	Aug.	S.N.E.
	16-30	−33.0	−11.6	69.6	67.7	7	1970	
	31-60					3		
	61-180					1		
17	1-15					0	1954-63	S.N.E.
	16-30					3		
	31-60	−.2	−10.4	222.9	57.1	5		
	61-180					0		

[1]Positive values signify northward movement. Negative values signify southward movement.
[2]Positive values signify eastward movement. Negative values signify westward movement.
[3]New Jersey.
[4]Long Island.
[5]Southern New England.

Jersey or that the intensity of the southern New England fishery was greater than that off New Jersey. While the latter may be true, there may be alternative interpretations and additional analysis is required. It is also suggested that analysis be undertaken for tags returned after the season of release.

MORTALITY ESTIMATION

The number of recoveries per year from releases by year, months within years, and various groupings of years, months, and release locations were employed to estimate the survival rates for young bluefin in the middle Atlantic bight of North America. The first analyses were run using only the data employed to form the basic groups as defined in the migration analysis, thus eliminating some releases which were substantially different with respect to their location and/or time of release than for most of the fish tagged. Although this reduced the numbers of returns used, it probably did not greatly affect the estimates of mortality rates.

Method of Release

In all years since 1961, with the exception of 1963, tuna were captured for tagging by both sport and commercial gear (purse seine). In Table 3 the

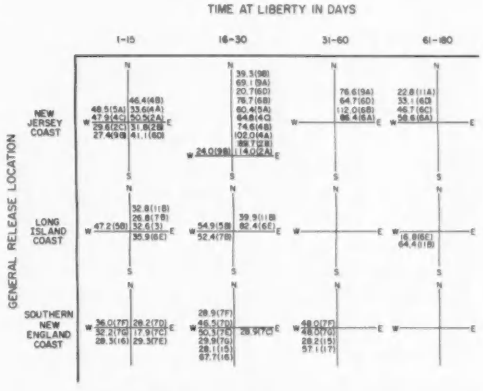

FIGURE 2.—Summary of mean distance and direction of migration of tagged bluefin tuna stratified by time at liberty and by general area of release. Distances are in nautical miles. Release group numbers are given in parentheses.

proportions of tagged fish returned were compared for the two methods of original capture. Five of the nine chi-square tests of the hypotheses of homogeneity indicate highly significant differences in the return percentages between the types of gear used to capture the tuna for tagging. When only the 5 yr with significantly different return rates for the types of gear, i.e., 1965, 1966, 1968, 1969, and 1970 are considered, higher return percentages were obtained for sport tagged fish in 4 of

TABLE 3.—Chi-square tests of equality of return probabilities between sport and commercial gear releases of tagged bluefin tuna in the northwestern Atlantic Ocean. Each test has 1 degree of freedom.

	Sport			Commercial			
Year	Release	Return	Return rate (%)	Release	Return	Return rate (%)	Chi-square value
1961	129	7	5.4	21	0	0	1.20
1962	52	4	7.7	25	0	0	2.03
1964	10	3	30.0	455	128	28.1	0.02
1965	43	17	39.5	1,629	244	15.0	19.18**
1966	187	84	44.9	3,772	1,094	29.0	21.60**
1967	14	3	21.4	614	183	29.8	0.46
1968	41	11	26.8	219	104	47.5	5.98*
1969	244	91	37.3	92	15	16.3	13.63**
1970	425	162	38.1	32	6	18.8	4.80*

**Significant at the 0.01 level.
*Significant at the 0.05 level.

the 5 yr. The data cannot be pooled over years to increase the numbers in individual cells in the chi-square tables since the recovery percentages and numbers tagged vary so greatly from year-to-year.

However, the Mantel-Haenszel test can be used to examine the data in toto (Snedecor and Cochran, 1967:255-256). The calculations resulted in a value of 8.89, which is highly significant. As is discussed in a later section, we think that most of the difference between return rates of sport and commercial tagged fish is caused by immediate tagging mortality. Immediate tagging mortality does not affect estimates of instantaneous total mortality. Therefore, we decided to use as much of the available data as possible and combined the data for estimates of mortality rates. Immediate tagging mortality does affect estimates of rates of exploitation and the components of mortality. Adjustments were made in an attempt to remove the effects of immediate tagging mortality and tag shedding.

Total Mortality Estimates – Chapman and Robson Method

Following the notation of Bayliff and Mobrand (1972), the number of tags remaining on bluefin at time t (years) is given by

$$N_t = N_0 \pi \rho e^{-Zt} \quad (1)$$

where N_t = Number of tags remaining on bluefin at time t
N_0 = number of released tags
π = portion of bluefin which remain alive after Type-I, immediate, tagging mortality takes place
ρ = portion of tags which are retained after Type-I shedding takes place
Z = instantaneous total losses on an annual basis.

$$Z = F + X$$

where F = instantaneous fishing mortality on an annual basis
X = instantaneous other losses on an annual basis.

$$X = M + G + L + E$$

where M = instantaneous natural mortality on an annual basis
G = instantaneous Type-II tagging mortality on an annual basis
L = instantaneous Type-II tag shedding on an annual basis
E = instantaneous emigration from fishing grounds on an annual basis.

The number of tags returned during a year is given by

$$n_t = \frac{FcN_t}{Z}(1 - e^{-Z}) \quad (2)$$

where n_t = number of tags returned between t and $t + 1$
c = portion of recovered tags that are returned.

Many assumptions are implicit in the above model. An exponential model is assumed to be

correct. It is assumed that all instantaneous shedding, mortality, and emigration rates are constant—within years and among years. Since fishing was concentrated during the summer season, the assumption of constant fishing mortality is not valid. Also fishing effort probably varied over the years of the study. Available measures of fishing effort are thought to be inaccurate but were used in the last part of the analysis. The validity of the assumption of constant rate of emigration is not known, but tag returns suggest that transatlantic migrations are sporadic. This suggests that the assumption of constant emigration is not valid. While we recognize that some of our assumptions probably are invalid, it is our judgment that the effect of the violations on our results is not serious.

For the first part of the analysis we assumed that c, π, and ρ equal one. In the first analysis minimum variance unbiased estimates of the total annual survival rates were computed by the method developed by Chapman and Robson (1960) for the recovery data by year pooled in a variety of different ways over release categories. Confidence intervals were computed for s, the fraction surviving per year, and Z, the associated instantaneous mortality rate. A chi-square test was used to determine if the number of recaptures in the first recovery period is compatible with the survival pattern exhibited by the rest of the data, i.e., if the hypothesis of constant F and X is true. This test was applied sequentially, i.e., the second year was defined as the first recapture category and the test repeated until either all recapture years were eliminated or a survival rate was obtained from some subset of the data. For all releases the tagging year was taken as the first recapture category at the start of the analysis. The results of the survival rate computations are shown in Table 4 for the following data groupings:

1) Over all years
2) Over three adjacent release years
3) Individual years
4) July releases for three adjacent release years
5) Individual months within years
6) Release groups as defined in Table 1.

An obvious feature of this analysis is that in many of the recapture series, the numbers recovered the first year or two were higher than expected from the entire recapture series. This result is somewhat surprising because it might be expected that the number recaptured the first year would be underrepresented because of less exposure to the fishery. Three possible factors that could have caused the higher than expected recaptures in the first year or two after release are:

1) Tagged fish were released into an area where fishing activity was concentrated.
2) The proportion of the population migrating into the fishing area decreased as the fish became older; thus the availability of the tagged fish in the fishing area may have fallen off rapidly enough in later years to have caused a disproportionate number of recaptures in the first and second years after release.
3) The method of estimation assumes constant fishing mortality rates and other loss rates; variability in recovery effort could have caused the number of recaptures per year to deviate from a simple exponential decline with time.

Several aspects of the data emerge from Table 4. The estimates of survival rates are low but highly erratic; restricting the releases to finer time-location grids did not improve the stability of the estimates as might be expected. Since no time trend in survival is evident, pooling over years is a useful device to average out some of the fluctuations in the data. In one sense this is a substitute for use of recapture effort statistics and working with the number of recoveries per unit of recovery effort. The recaptures per year were combined over years using various weighting factors to develop adjusted numbers recaptured per year. None of these weighting schemes offered an improvement in the use of the simple unweighted average percent recapture per year at liberty for the years 1964-68. The proportion surviving per year as estimated from the simple average of the percentages was 0.188. This value is well within the confidence interval of the s-value of 0.231 estimated from the actual numbers pooled over all years. For the latter estimate, however, we did not use the recoveries made during the first 2 yr at liberty.

Inclusion of the first two recapture periods in the Chapman-Robson analysis, particularly for the last set of release groups which are fairly homogeneous, had the general effect of reducing the survival estimates. The numbers of recaptures

TABLE 4.—Survival rate estimates for various release group categories of tagged bluefin tuna.

Type of group[1]	Group	Recapture years used in s and Z computation	s(95% confidence interval)	Z(95% confidence interval)
1	All	[2](1, 2), 3, 4, 5	0.231 (.16, .30)	1.44 (1.14, 1.75)
	1963-65	-	Not constant (NC)	
	1964-66	[2](1, 2), 3, 4, 5	.174 (.09, .26)	1.70 (1.23, 2.16)
[1]2	1965-67	(1)[1], 2, 3, 4, 5	.118 (.10, .14)	2.13 (1.93, 2.32)
	1966-68	[2](1, 2), 3, 4, 5	.254 (.14, .37)	1.32 (0.88, 1.77)
	1967-69	[2](1), 2, 3, 4	.103 (.04, .17)	2.19 (1.60, 2.79)
	1968-70	-	NC	
3	1964	-	NC	
	1965	1, 2, 3, 4	.343 (.29, .39)	1.07 (.93, 1.21)
	1966	[2](1, 2), 3, 4, 5	.233 (.14, .32)	1.42 (1.03, 1.81)
	1967	(1)[1], 2, 3, 4	.323 (.24, .41)	1.11 (0.86, 1.37)
	1968	1, 2, 3	.243 (.17, .31)	1.39 (1.11, 1.68)
	1969		NC	
	July 1963-65	1, 2, 3	.146 (.10, .19)	1.90 (1.61, 2.19)
	July 1964-66	[2](1, 2), 3, 4, 5	.400 (.20, .60)	0.87 (0.39, 1.34)
4	July 1965-67	[2](1, 2), 3, 4, 5	.355 (.18, .53)	0.99 (0.51, 1.46)
	July 1966-68	[2](1, 2), 3, 4, 5	.367 (.19, .55)	0.96 (0.49, 1.42)
	July 1967-69	1, 2, 3, 4	.246 (.19, .30)	1.39 (1.17, 1.61)
	July 1968-70	-	NC	
	July 1964	1, 2	.128 (.06, .19)	2.00 (1.50, 2.49)
	Aug. 1964	-	NC	
	July 1965	1, 2, 3	.160 (.11, .21)	1.81 (1.48, 2.13)
	Aug. 1965	-	NC	
[3]5	July 1966	[2](1, 2), 3, 4, 5	.407 (.21, .60)	0.85 (0.40, 1.30)
	Aug. 1966	[2](1, 2), 3, 4, 5	.085 (.05, .12)	2.43 (2.08, 2.79)
	July 1967	1, 2, 3, 4	.244 (.18, .31)	1.39 (1.13, 1.66)
	Aug. 1967	-	NC	
	July 1968	1, 2, 3	.201 (.13, .27)	1.57 (1.23, 1.92)
	July 1969	-	NC	
	Aug. 1969	-	NC	
	G1	1, 2, 3, 4	.582 (.45, .72)	0.53 (0.31, 0.75)
	G2A	1, 2	.189 (.06, .32)	1.57 (0.90, 2.24)
	G2B	1, 2	.065 (.00, .15)	2.45 (1.10, 3.79)
	G2C	1, 2	.160 (.01, .31)	1.68 (0.78, 2.58)
	3	-	NC	
	4A	1, 2, 3	.190 (.07, .31)	1.57 (0.95, 2.20)
	4B	1, 2, 3	.165 (.09, .24)	1.75 (1.30, 2.21)
	4C	1, 2	.083 (.00, .18)	2.27 (1.18, 3.36)
	5A	-	NC	
	5B	-	NC	
	5C	-	NC	
	6A	-	NC	
	6B	-	NC	
	6C	-	NC	
	6D	-	NC	
6	6E	-	NC	
	7A	-	NC	
	7B	[2](1, 2), 3, 4, 5	.375 (.01, .74)	0.88 (0.04, 1.71)
	7C	[2](1), 2, 3, 4	.083 (.01, .16)	2.34 (1.49, 3.19)
	7D	-	NC	
	7E	-	NC	
	7F	-	NC	
	7G	-	NC	
	8	[2](1), 2, 3, 4	.125 (.00, .26)	1.88 (0.83, 2.94)
	9A	1, 2	.154 (.01, .30)	1.72 (0.82, 2.62)
	9B	1, 2, 3, 4	.205 (.13, .28)	1.55 (1.19, 1.92)
	10	-	NC	
	11A	1, 2, 3	.357 (.17, .54)	0.98 (0.48, 1.47)
	11B	1, 2, 3	.240 (.12, .36)	1.37 (0.87, 1.87)
	12	-	NC	
	13	-	NC	
	14	-	NC	

[1]Includes tags assigned by cruise number.
[2]Recapture years eliminated by chi-square test of full recruitment to tagged population are shown in parentheses.
[3]July results include tags assigned by cruise number.

dropped off so rapidly, however, after the first two recapture periods that little reliability can actually be placed on estimates using only data from the tail end of the time series.

This first examination of the recaptures by time at liberty was followed by a revised analysis of the July releases each year and all releases each year for 1964 through 1968. An attempt to include all tags in the analysis was made by assigning tags without recorded release dates to most likely release dates by means of the accompanying information, e.g., by cruise number. For the most part this revision produced minor changes in the estimates of total survival rates. Raw exploitation rates were estimated from the total number of recaptures per release using all data whether or not any information was available on date of recapture.

Estimates of Fishing and Other Losses

We used the following equations to estimate rates of exploitation, fishing, and other losses:

$$\hat{u}_T = R/N_0$$

where $\hat{u}_T$ = estimate of total exploitation of tagged bluefin tuna over n years

R = number of tag returns.

$$\hat{u}_1 = \hat{u}_T / \sum_{i=0}^{n} \hat{s}^i$$

where $\hat{s}$ = survival rate estimated from revised data by the Chapman-Robson method

$\hat{u}_1$ = estimate of single season exploitation of tagged bluefin tuna.

$$\hat{F} = \hat{u} \quad (-\ln \hat{s})/(1 - \hat{s})$$

$$\hat{X} = \ln(\hat{s}) - \hat{F}$$

These estimates for July releases are shown in Part A of Table 5, and in Part B of the same table, estimates of the same set of parameters for all releases are given with the exception of the single season exploitation rates. We believe that distributing the releases during the entire fishing season, rather than restricting them to the first part of the season, July, makes it impossible to estimate a single season exploitation rate. It will be noted that the actual observed exploitation rates are high, especially in view of the fact that no corrections were made for either immediate tagging mortality, tag shedding, or nonreporting. The total recapture percentages range from 16% to 48%.

Lenarz et al. (1973) estimated that the rate of immediate tag shedding $(1 - \rho)$ for Atlantic bluefin tuna is 0.027 and that the instantaneous rate of tag shedding (L) is 0.310. Their estimates were used to correct our estimates of exploitation and mortality rates for shedding as follows:

TABLE 5.—Estimates of total survival, rate of exploitation, fishing mortality rate and total other loss rate of tagged bluefin tuna for July releases and for all releases by year of release.

Item	1964	1965	1966	1967	1968
Part A. July releases only:					
(N) Numbers released	397	951	2,047	448	226
(R) Numbers recovered	96	169	461	131	108
$\hat{s}$	0.128	0.160	0.407	0.244	0.201
$\hat{u}_1$	0.211	0.150	0.143	0.224	0.385
$\hat{u}_T$	0.242	0.178	0.225	0.292	0.478
$\hat{F}$	0.497	0.327	0.217	0.418	0.773
$\hat{X}$	1.558	1.506	0.697	0.999	0.838
$(\hat{F} + \hat{X})$	2.056	1.833	0.899	1.411	1.604
Part B. All releases by year:					
(N) Numbers released	465	1,672	3,959	628	260
(R) Numbers recovered	132	262	1,177	187	116
$\hat{s}$	0.196	0.343	0.233	0.323	0.243
$\hat{u}_T$	0.284	0.157	0.297	0.298	0.446
$\hat{F}$	0.463	0.168	0.433	0.337	0.631
$\hat{X}$	1.167	0.902	1.024	0.793	0.784
$(\hat{F} + \hat{X})$	1.630	1.070	1.457	1.130	1.415

$$(\hat{F} + \hat{X})^* = \hat{F} + \hat{X} - L$$

where $(\hat{F} + \hat{X})^*$ = estimate of total instantaneous apparent mortality corrected for tag shedding rate,

$$\hat{s}^* = e^{-(\hat{F} + \hat{X})^*}$$

where $\hat{s}^*$ = estimate of annual survival corrected for shedding rate,

$$\hat{u}_T^* = \hat{u}_T/\hat{\rho}$$

where $\hat{u}_T^*$ = estimate of total exploitation of tagged bluefin tuna corrected for immediate tag shedding,

$$\hat{u}_1^* = \hat{u}_1/\hat{\rho}$$

where $\hat{u}_1^*$ = estimate of seasonal exploitation corrected for immediate tag shedding,

$$\hat{F}^* = \hat{u}_1^* \ (-\ln s)/(1 - \hat{s})$$

where $\hat{F}^*$ = estimate of F corrected for immediate tag shedding,

$$\hat{X}^* = -\ln(\hat{s}^*) - \hat{F}^*$$

where $\hat{X}^*$ = estimate of X corrected for immediate tag shedding,

$$\hat{u}_1^{**} = \frac{\hat{F}^*}{\hat{F}^* + \hat{X}^*} \ (1 - \hat{s}^*)$$

where $\hat{u}_1^{**}$ = estimate of single season exploitation of tagged and untagged bluefin corrected for all tag shedding, and

$$\hat{u}_T^{**} = \hat{u}_1^{**} \sum_{i=0}^{n} (\hat{s}^*)^i$$

where $\hat{u}_T^{**}$ = estimate of total exploitation of tagged and untagged bluefin corrected for all tag shedding.

The estimates are shown in Table 6. Estimates of $\hat{X}^*$ (other losses) range from 0.366 to 1.234 (average = 0.792). The estimates of $\hat{X}^*$ are considerably higher than expected values of M (natural mortality) for bluefin. Bluefin are very long-lived fish and values of M of 0.1 to 0.2, if M is constant, would seem reasonable. Thus, there may be significant amounts of Type-I (immediate) and Type-II (long-term) tagging mortality, nonreporting, and/or apparent mortality caused by emigration.

TABLE 6.—Estimates of rates of exploitation and mortality of bluefin tuna corrected for tag shedding.

Item	1964	1965	1966	1967	1968
$(\hat{F} + \hat{X})^*$	1.746	1.523	0.589	1.101	1.294
$\hat{s}^*$	0.174	0.218	0.555	0.333	0.274
$\hat{u}_T^*$	0.249	0.183	0.231	0.300	0.491
$\hat{u}_1$	0.217	0.154	0.147	0.230	0.396
$\hat{F}^*$	0.512	0.336	0.223	0.429	0.795
$\hat{X}^*$	1.234	1.187	0.366	0.671	0.499
$\hat{u}_1^{**}$	0.242	0.172	0.168	0.260	0.446
$\hat{u}_T^{**}$	0.284	0.218	0.342	0.388	0.611

It seems plausible that some Type-I tagging mortality exists. In an earlier section it was noted that, more returns were obtained from sport gear releases than from commercial gear releases. Statistically significant, more returns were obtained from sport releases than commercial releases in 1965, 1966, 1969, and 1970. A possible cause of the difference in return rates could be that sport tagged bluefin are of different ages than commercially tagged bluefin. Bluefin of different ages could suffer different rates of tagging mortality and shedding, and could behave differently. Data have not been compiled in a fashion that allows examination of the age at release by the two gear types. We recommend that it be and assume for the present that age-dependent effects are negligible. The differences in return rates could also be caused by Type-I tagging mortality. Experienced taggers report that sport-gear-caught bluefin appear to be in better condition than those caught by commercial gear. Also, commercial gear tends to capture entire schools of bluefin while sport gear captures one bluefin at a time. Thus, bluefin released from sport gear tend to be released into the immediate area of a school of bluefin while bluefin released from commercial gear are not. There may be an advantage for bluefin to be in a school. Bayliff (1973) found that return rates of purse-seine-caught yellowfin tuna tagged immediately after a set is made can be more than two times higher than yellowfin tagged at a later time (Table 7). This evidence suggests that Type-I tagging mortality is very important

TABLE 7.—Releases, returns, and percentages of return of yellowfin tuna for IATTC[1] Cruise 1055, by time between commencement of tagging and release of fish (from Bayliff, 1973).

Time (min)	Number released	Number returned	% returned
0-10	1,920	277	14.4
10-20	1,972	195	9.9
20-30	1,563	86	5.5
30-40	1,145	47	4.1
40-50	934	44	4.7
>50	975	23	2.4
Total	8,509	672	7.9

[1]Inter-American Tropical Tuna Commission.

for purse-seine-caught yellowfin tuna. Bayliff[6] (pers. commun.) believes that bluefin tuna are more hardy than yellowfin tuna and thus expects that Type-I tagging mortality is lower for bluefin than for yellowfin.

Assuming that sport releases suffered insignificant amounts of Type-I tagging mortality and using the Mantel-Haenszel weighting procedure, the 1964-68 average Type-I tagging mortality for commercial tagged fish was 21%. During this period, 96% of the releases were commercial tagged fish. The average Type-I tagging mortality for all releases during 1964-68 was 20%.

The rates of exploitation and mortality were corrected for Type-I tagging mortality as follows:

$$\hat{u}_T^{***} = \hat{u}_T^{**}/\pi$$

where $\hat{u}_T^{***}$ = estimate of total exploitation corrected for shedding and Type-I tagging mortality,

$$\hat{u}_1^{***} = \hat{u}_1^{**}/\pi$$

where $\hat{u}_1^{***}$ = estimate of seasonal exploitation corrected for shedding and Type-I tagging mortality,

$$\hat{F}^{**} = \hat{u}_1^{***}\,(-\ln \hat{s}^*)/(1 - \hat{s}^*)$$

where $\hat{F}^{**}$ = estimate of F corrected for shedding and Type-I tagging mortality, and

$$\hat{X}^{**} = -\ln(\hat{s}^*) - \hat{F}^{**}$$

where $\hat{X}^{**}$ = estimate of X corrected for shedding and Type-I tagging mortality.

The estimates are shown in Table 8. The values of $\hat{X}^{**}$ range from 0.300 to 1.109 (average = 0.678) and are still higher than the expected rate of natural mortality for bluefin. The large difference between values for 1964-65 and the values for 1966-68 is worth noting. Food and Agriculture Organization (1972) reports that a relatively large number of bluefin tuna tagged in the northwest Atlantic in 1965 were recovered in the Bay of Biscay during the following year. This suggests that a large-scale transatlantic migration occurred between the 1965 and 1966 fishing seasons. Thus migration from the fishery is a plausible explanation for a portion of $\hat{X}^{**}$.

TABLE 8.—Estimates of rates of exploitation and mortality for northwest Atlantic bluefin tuna. The rates have been corrected for tag shedding and a hypothetical value of Type-I tagging mortality.

	1964	1965	1966	1967	1968	Average
u_T^{***}	0.355	0.272	0.428	0.485	0.764	[1]0.456
u_1^{***}	0.302	0.215	0.210	0.325	0.558	[1]0.327
F^{**}	0.639	0.419	0.278	0.536	0.995	0.573
X^{**}	1.110	1.104	0.311	0.564	0.300	0.678

[1]Calculated from averages of F^{**} and X^{**}.

Total Mortality Estimates – Regression Method

We next used available effort data for examining the effect of changes in effort on our estimates of mortality. The effort data were obtained from inquiries and logbooks of purse seiners that participated in the commercial fishery for bluefin in the northwestern Atlantic. The data have not been standardized by vessel class. We question the validity of the data as a measure of fishing effort, i.e., proportional to F, because a varying portion of the fleet relied heavily on airplane scouting. Conversion of the data to a standard unit of effort is worth a study in itself and we recommend that such a study be carried out.

In another attempt to estimate total mortality the natural logarithm of the number of returns per unit effort (Table 9), taking the number of boat-days recorded per season as a legitimate measure of effort, was regressed on time as measured to the center of each year following the release. An exact

[6]Bayliff, W. H. Inter-Am. Trop. Tuna Comm., P. O. Box 271, La Jolla, CA 92037.

TABLE 9.—Returns of tagged bluefin tuna per boat-day by years at liberty.

Year	0	1	2	3	4
Part A. July releases only:					
1964	0.0902	0.0344			
1965	0.3538	0.0968	0.0374		
1966	0.9839	1.3957	0.1059	0.0526	0.0111
1967	0.5080	0.3647	0.0421	0.0037	
1968	1.0235	0.1579	0.0222		
Part B. All releases:					
1964	0.1100	0.0786			
1965	0.4029	0.3280	0.1925	0.0718	
1966	2.8495	3.1016	0.6235	0.0842	0.0222
1967	0.5241	0.7059	0.1684	0.0481	
1968	1.0353	0.2000	0.0333		

analytical formulation of this mortality model has two independent variates—cumulative time and cumulative effort. Not only are these two variables so highly correlated that it is virtually impossible to obtain useful estimates of the two regression coefficients, but also there are too few data points available for multiple regression analysis. The regression coefficient of the simple cumulative time regression is a crude measure of the total mortality rate. The fitted regression lines are shown in Figure 3 for July releases and in Figure 4 for all releases for each year. The values of the coefficients are given in Table 10.

With the exception of 1966, when the returns per boat-day increased during the year following release (and the data were eliminated from the regression), the logarithms of the recaptures per unit effort decrease in a linear fashion and it is clear the regressions provide reasonable fits to the data points. Seven of the eight estimated survival rates shown in Table 10 are lower than their counterparts in Table 5. Both of these analyses provide at best only crude approximations of the true survival rates; however, they do show fair general agreement. The catch-per-effort estimates indicate the loss rates are tending to increase with time.

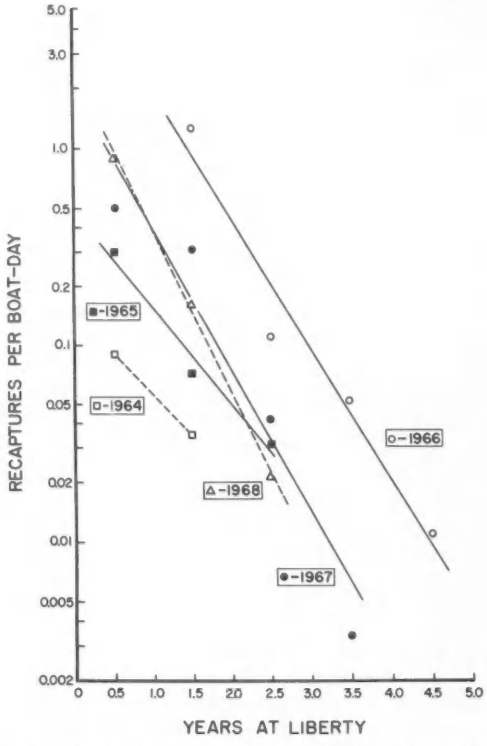

FIGURE 3.—Regression of recaptures per boat-day vs. time at liberty for July releases of tagged bluefin tuna.

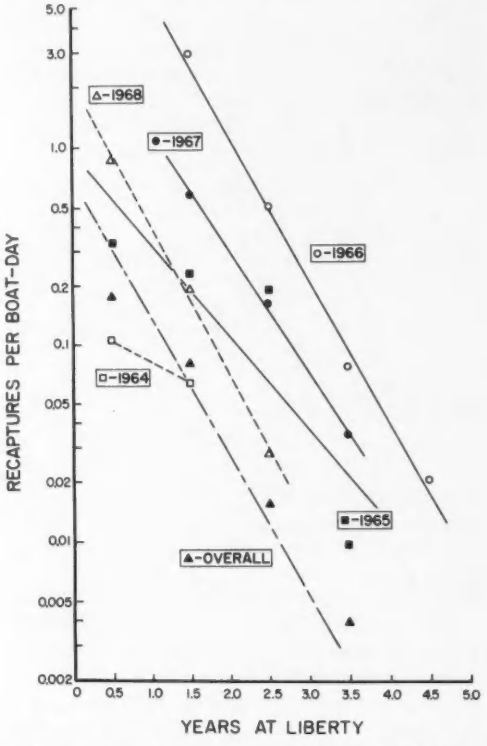

FIGURE 4.—Regression of recaptures per boat-day vs. time for all releases, by year, of tagged bluefin tuna.

TABLE 10.—Estimates of total survival rates of tagged bluefin tuna from regression analysis of return per unit-of-effort data.

	July releases only		All releases	
Year	Z	s	Z	s
1965	1.12	0.33	1.08	0.34
1966[1]	1.51	0.22	1.68	0.19
1967	1.70	0.18	1.41	0.24
1968	1.87	0.15	1.73	0.18
Average[2]	1.55	[3]0.21	1.48	[3]0.23

[1]Recaptures in release year not included in 1966 regression analysis.
[2]Regression estimates using average unweighted percentage returns for 1964-68 are: $Z = 1.67$ and $s = 0.19$. This estimate happens to be exactly the same as the estimate of $Z = 1.67$ = (average time at liberty) $^{-1}$ where average time at liberty is 0.60 yr.
[3]Survival rate computed from average Z-value.

DISCUSSION

Exactly what these "survivals" are measuring is of prime interest. They are properly thought of as the results of disappearance rates which are composed of mortalities (F, M, and G), tag shedding, and changing migratory patterns with age. Apparently few of the older fish entered the surface fishery in the western north Atlantic during the period of the study and the decreasing proportion of the population that entered the fishery is a primary factor lowering the apparent survival. In 1966 when the fish tagged were significantly younger than in the other years—having an average age of 1.4 yr as opposed to average ages of at least a year older in other tagging years—the greatest return of tags occurred during the year after release. For these younger bluefin, a higher proportion returned to the fishing area the year after they were released than for the older tagged fish.

The exploitation rate on the tagged fish was exceedingly high when they were in the fishery. The high fishing mortality rates in Table 8 may underestimate the true rates for tagged bluefin; most of the various sources of error that may bias these estimates act to decrease the estimate of the fishing rate relative to its true value. However, it is known that bluefin available to the northwest Atlantic fisheries are not a closed population. Tagging studies have revealed transatlantic migrations to and from the fishery. Migration could also occur from the middle Atlantic. Thus it must still be determined whether the high exploitation rate applied to the population or just to the portion of the population that entered the fishery. Ricker (1958:35) describes the effects of tagging fish that are more vulnerable to fishing than other members of the population. "Again, if fish of certain sizes are more vulnerable than others, a Peterson tagging experiment is apt to overemphasize the vulnerable ones both in respect to tags put out and recaptures made; hence the estimate of rate of exploitation is too high and the population estimate is too low." Future analysis stratifying the data by age at release would help to answer some questions that arise because of the migratory behavior of bluefin. We suggest cohort analysis in the fashion of Bayliff (1971) as a productive method of analysis.

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the Fisheries Research Board of Canada, the Food and Agriculture Organization of the United Nations, and many other national and private research organizations have assisted in the promoting of the tagging of fishes, and the return of tags with recapture data.

The tagging results were made possible by the thousands of anglers, captains, and mates who have tagged, and released many of their catches, the commercial tuna fishermen who have cooperated with the tagging program, and the clubs, committees and individuals who have encouraged tagging. We regret that space does not permit individual acknowledgments here; the major participants are listed in the informal progress reports which are issued periodically by the Woods Hole Oceanographic Institution. The press and the broadcasting media have also done much to encourage tagging and the return of tags.

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FEEDING RELATIONSHIPS OF TELEOSTEAN FISHES ON CORAL REEFS IN KONA, HAWAII

EDMUND S. HOBSON[1]

ABSTRACT

Feeding relationships of teleostean fishes on coral reefs at Kona, Hawaii, were studied during 1969 and 1970.

Fishes that have a generalized feeding mechanism, including those carnivores whose morphologies place them close to the main line of teleostean evolution, are predominantly nocturnal or crepuscular. These include holocentrids, scorpaenids, serranids, apogonids, priacanthids, and lutjanids. The major prey of the nocturnal species are small, motile crustaceans, which are most available to the direct attacks of generalized predators when they leave their shelters after dark. The major prey of the crepuscular species are smaller fishes, whose defenses against direct attacks of generalized predators are less effective during twilight. Feeding by generalized predators during the day depends largely on being within striking distance of prey that make a defensive mistake, a position best attained by those predators that ambush their prey from a concealed position, or by those that stalk.

Ambushing and stalking tactics have produced some highly specialized forms that, during the day, prey mostly on smaller fishes. Diurnal ambushers include the highly cryptic synodontids, scorpaenids, and bothids; diurnal stalkers include aulostomids, fistulariids, belonids, and sphyraenids—all of them long, attenuated fishes.

Some predators—most notably the muraenid eels—are specialized to hunt deep in reef crevices, and here they capture some of the many small animals that shelter themselves in those crevices, day and night, when resting, injured, or distressed. Mullids use their sensory barbels to detect small animals that have sheltered themselves amid the superficial covering on the reef, or in the surrounding sand; at least some mullids further use their barbels to drive these prey into the open.

Most of the fishes on Kona reefs are among the more highly evolved teleosts, having reached, or passed, the percoid level of structural development. The adaptability of the feeding apparatus in these more advanced groups has given rise to a wide variety of specialized species, including both carnivores and herbivores, that have diverged from one another mostly on the basis of differing food habits. These fishes, most of which are diurnal, include the chaetodontids, pomacentrids, labrids, scarids, blenniids, acanthurids, and *Zanclus*, among the perciforms; and the balistids, monacanthids, ostraciontids, tetraodontids, canthigasterids, and the nocturnal diodontids, among the tetraodontiforms. With their specialized feeding structures and techniques, these fishes consume organisms like sponges, coelenterates, large mollusks, tunicates, and tiny or cryptic crustacea that are protected by behavioral or anatomical features from fishes not appropriately specialized.

Many important ecological relations among marine fishes are understood only by considering in broad overview during both day and night the different forms living together under natural conditions. With this in mind, I undertook a broad study of reef fishes at Kona, Hawaii, between June 1969 and August 1970. A segment of this study dealing with the twilight situation was published earlier (Hobson, 1972). The present report describes the situations that prevail throughout day and night. The work is centered on direct observations of activity in the fishes, as was my earlier study of predatory behavior of shore fishes in the Gulf of California (Hobson, 1968a), but here with greater emphasis on detailed analysis of food habits.

Several other workers adopted broad overviews in considering fishes of various areas. Limbaugh (1955) studied fishes in California kelp beds during the day, whereas Starck and Davis (1966) described the habits of fishes in the Florida Keys at night; both of these studies present extensive direct observations of activity, but little data on food habits. On the other hand, Hiatt and Strasburg (1960), as well as Randall (1967), and Quast (1968), treated extensively the food habits of fishes collected during daylight in the Marshall Islands, the West Indies, and southern California, respectively, but offered relatively few direct observations of activity. Suyehiro (1942) comprehensively treated the feeding morphology of fishes in Japan

[1]Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 98, Tiburon, CA 94920.

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and included data on food habits; however, he included little information on activity. The 1970 United States Tektite II program provided many scientists with the opportunity to make direct observations on a Virgin Island reef, and reports concerning the fishes have been published in one volume (Collette and Earle, 1972). Many other reports of limited scope are scattered through the literature, most of them being fragmented data on food habits; nevertheless, accounts of activity based on direct observations are sparse, especially of nocturnal activity.

The great variety of feeding mechanisms for which teleostean fishes are so well known occur among coral-reef fishes far more so than among the fishes of any other habitat. I take advantage of this circumstance in the discussion that concludes the present report and consider the feeding relationships among fishes on Kona reefs in the context of teleostean evolution.

METHODS

Direct Observations

I observed activity of the fishes during 632 h underwater at all periods of day and night using scuba and by snorkeling. Except when collecting specimens, I tried not to influence the fishes or their environment, hoping that events were taking a natural course. Fishes considered in this report are those that can be seen by an underwater observer at some time during day or night. Although this includes by far most of the reef fishes, some abundant species are not included because they remain secreted in the reef at all hours.

Food Habits

The gut contents of 1,547 fish specimens of 102 species were analyzed. With a few isolated exceptions, noted below, all the specimens were collected with spears. I find spearing the most effective way to collect fishes for study of food habits. Using this method, specimens were collected in specific locations at the times of day and night that best define diurnal-nocturnal activity patterns. Because I speared all the specimens myself, I know what each individual was doing when captured, and this knowledge significantly influenced analysis of the data. Even the response of the various fishes to being stalked and speared (or missed) provided certain behavioral insights.

Food habits change over the life of at least most fishes, usually along with recognizable changes in behavior and morphology. Unless otherwise indicated, specimens selected for this study showed behavior and morphology judged typical of adults.

The collections were spread over time and space, so that possible effects of transient localized, perhaps atypical, situations were reduced. Generally, only a single individual of any one species was collected during a single period of observations; thus, for a given species, most individuals each represent a separate collecting station. For these reasons, I judge the data from the food habit analysis to accurately represent the situation existing on Kona reefs over the 15 mo of this study.

The collections were spaced throughout day and night, so that relative digestion of gut contents supplements direct observations of activity in determining specific feeding times. All specimens were sealed in individual plastic bags immediately after being speared, most while still underwater. Gut contents of specimens collected while snorkeling were preserved immediately by injecting a concentrated formaldehyde solution directly into the gut cavity, whereas gut contents of fishes taken by scuba were preserved as soon as possible after emerging from the water. I was unable to see a difference in the digestion undergone by material collected in each of these two ways, suggesting that digestion is sharply curtailed by the death of the fish. Where practical, identifications of items in the guts were carried far enough to establish such general prey characteristics as habitat and mode of life.

Quantifying Food Habits

For those species represented by enough numbers in the analysis of gut contents, I state: 1) the number of fish of that species containing each food item, and 2) the mean percent of that item in the *diet volume,* which is the total volume of gut contents in all specimens of that species. This second figure was calculated from estimates of the percent each item taken by the species contributed to the gut contents of each individual fish (0 to 100%). The food items are listed in order of a *ranking index,* which is computed by multiplying the ratio of fish containing the item to the number of fish sampled, by the mean percent that item represented of the diet volume. Thus, for example, for *Holocentrus sammara* (Table 10), the number one prey, xanthid crabs, has a ranking index of

$12/17 \times 52.5 = 37.05$. The data are tabulated when there are more than a few items in the gut contents of a given species.

In species with a well-defined stomach, usually only stomach contents were analyzed, as materials in the intestines generally were too far digested for satisfactory analysis. On the other hand, some fishes that do not have a well-defined stomach have much material in their intestine that is suitable for study, and so was included in the analysis. Thus data sometimes are specified as being from stomach contents, but at other times the more general term gut contents is used.

Transect Counts

To characterize the fishes inhabiting each of the various inshore habitats described below, 100-m transect lines were established in locations judged typical of each habitat. Twenty-two counts of fishes within 5 m of transect lines at 17 sites representing five habitat categories (see below) were made between September 1969 and May 1970; at least 1 mo passed between counts in any one habitat.

Quantifying Relative Abundance

In the Tables below that present data from the transect counts, the relative abundance of the different species is represented by a relative abundance index. This is the percentage that species represented of all fishes (individuals) counted along all transect lines in that habitat.

Assessing Nocturnal Colorations

A number of species possess distinctive day and night differences in coloration. Earlier (Hobson, 1968b), I discussed the problem of distinguishing true nocturnal hues from those elicited as a response to the diving light—a frequent source of error in literature reports of nocturnal color patterns. No color pattern that becomes intensified under the diving light is considered here to be a nocturnal pattern; the vast majority described herein were in fact almost immediately lost when the fish was illuminated.

Study Area

The study area extends 7.7 km along the southwestern shore of the Island of Hawaii, from Keawekaheka Point just north of Kealakekua Bay, to Alahaka Bay, south of Honaunau (Figure 1). This is part of what is known as the Kona coast. Except for short stretches of sand and cobble beaches at Napoopoo and Keei, the shoreline is a rough basalt face that drops abruptly into the sea from 2 to 3 m above the water's surface (Figure 2), to a similar depth below. From the base of this face the sea floor slopes down to water depths of about 20 to 30 m, about 50 to 600 m from shore, then falls away sharply to much greater depths. Thus, along this coast water less than 20 m deep is limited to a relatively narrow shelf, the outer rim of which provided a convenient natural boundary to the study area (Figure 1).

Environmental conditions in Kona are remarkably constant, which greatly aided this study. Surface water temperatures ranged from 29°C in the fall to 22°C in the spring, but I noted no marked seasonal variations among the fishes either in their activity or species composition. Conditions

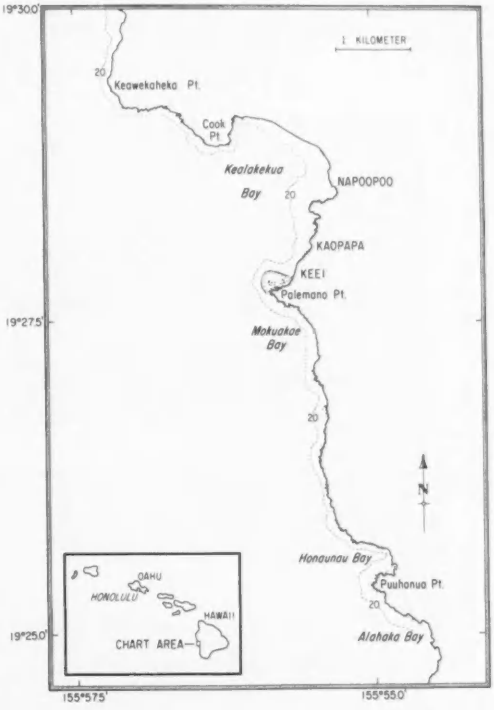

FIGURE 1.—The study area along the Kona coast, Island of Hawaii. Adapted from C. & G.S. chart 4123. Depth contour in meters.

are especially moderate on the Kona coast, in part because towering volcanoes shelter the area from the trade winds.

THE INSHORE HABITATS AND THEIR CHARACTERISTIC FISHES

The study area in Kona encompasses a variety of submarine habitats, each with a distinctive assemblage of fishes. For convenience, these habitats are here grouped subjectively into five categories: 1) coral-rich habitat, 2) boulder habitat, 3) shallow reef-flat habitat, 4) reef-face habitat, and 5) outer drop-off habitat. Along with the following habitat descriptions, there are listed the 10 fish species most often seen in each habitat, as observed in the transect counts.

Coral-Rich Habitat

In many places where there is shelter from the long Pacific swells, the sea floor in water between 2 and 12 m deep is richly overgrown with corals (Figure 3). The predominant coral is *Porites pukoensis,* which grows in a variety of massive formations. Examples occur in Honaunau Bay, in the lee of Palemano Point, and in the sheltered waters on the north side of Kealakekua Bay (Figure 1). Overall in the parts of the study area that are richly overgrown with corals, *P. pukoensis* variably shares dominance with another form, *P. compressus,* that grows as fingerlike branches 10 to 20 mm in diameter. *Porites compressus* is dominant where there is increased exposure to the prevailing swell, but where there is still some protection from a lee shore or increased water depth. Thus, in the middle of both Kealakekua Bay and Honaunau Bay, as well as in much of the study area where the water is more than about 15 m deep, broad fields of fingerlike *P. compressus* dominate the scene. In extreme situations, habitats dominated by either one of these coral forms are as distinct from one another in their characteristic faunas as any two habitat types characterized here. I group the two coral habitats together because in most of the coral-rich areas where observations were made during this study

FIGURE 2.—The shoreline at Cook Point, Kealakekua Bay (looking southeast), which is typical of the shoreline throughout most of the study area.

FIGURE 3.—Coral-rich habitat. Fishes shown include: *Chaetodon multicinctus, Ctenochaetus strigosus, Zebrasoma flavescens, Acanthurus nigrofuscus,* and *Zanclus canescens.*

the two forms of *Porites* share dominance. Nevertheless, the fishes listed in Table 1,[2] which are characteristic of those seen in the coral-rich habitat by day, were observed where *P. pukoensis* was the more dominant coral. Table 2[3] lists fishes characteristic of those seen in this same habitat at night. Because of difficulties inherent in making transect counts after dark, data in Table 2 are only rough approximations; they are presented primarily to illustrate the differing situation after dark, and to emphasize that the other counts reflect a situation characteristic of daytime only.

[2]Table 1 is based on data from five transects at four coral-rich sites—two at Honaunau, and two at Kaopapa in Kealakekua Bay (see Figure 1). Total number of species observed on these five transects: 82; mean number of individuals of all species for a single transect: 522.

[3]Table 2 is based on data from three nocturnal transects (one on a dark night, two on moonlit nights) at three coral-rich sites—two at Honaunau, one at Kaopapa in Kealakekua Bay (see Figure 1), all three of which were also used in daytime counts (Table 1). Counts were made by switching on a light briefly about every 10 m as we swam along the line. Listing of a species does not necessarily imply activity; as becomes clear in the species accounts, below, some of these fishes are inactive on or near the reef at night. Total number of species observed on these three transects: 36; mean number of individuals of all species for a single transect: 165.

Boulder Habitat

From shore to depths of about 15 m throughout that part of the study area lying off exposed shorelines, the sea floor is strewn with basalt boulders. Often these boulders are dotted with various algae and corals—mostly encrusting varieties—but because these forms are small, the

TABLE 1.—The 10 fish species most frequently seen along transect lines in the coral-rich habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 5$
1	*Ctenochaetus strigosus*	15.45	5
2	*Chromis leucurus*[1]	12.30	5
3	*Zebrasoma flavescens*	10.58	5
4	*Pomaentrus jenkinsi*	6.71	5
5	*Thalassoma duperrey*	5.71	5
6	*Chaetodon multicinctus*	4.41	5
7	*Acanthurus nigrofuscus*	4.37	5
8	*Acanthurus nigroris*	3.64	3
9	*Plectroglyphidodon johnstonianus*	3.07	5
10	*Centropyge potteri*	2.49	2

[1]In making transect counts I followed Gosline and Brock (1960) in recognizing *Chromis leucurus* to include two color forms. Further study may show that two (or more) species are included here (see species account for *C. leucurus* in this report).

FIGURE 4.—Boulder habitat. Fishes shown include: *Aphareus furcatus*, *Monotaxis grandoculis* (showing barred color pattern), *Acanthurus leucopareius*, and *Zebrasoma flavescens*.

TABLE 2.—The 10 fish species most frequently seen along transect lines in the coral-rich habitat at night.

Rank	Species	Relative abundance index	No. times in top 5 of individual transects $n = 3$
1	*Myripristis kuntee*	23.61	3
2	*Apogon menesemus*	14.52	3
3	*Myripristis murdjan*	12.33	2
4	*Apogon snyderi*	11.90	3
5	*Zebrasoma flavescens*	6.85	2
6	*Chaetodon multicinctus*	4.03	0
7	*Acanthurus sandvicensis*	2.40	1
8	*Acanthurus nigroris*	2.22	0
9	*Holocentrus lacteoguttatus*	1.21	0
10	*Chaetodon ornatissimus*	1.21	0

TABLE 3.—The 10 fish species most frequently seen along transect lines in the boulder habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 4$
1	*Acanthurus nigrofuscus*	13.74	4
2	*Ctenochaetus strigosus*	10.77	4
3	*Zebrasoma flavescens*	9.61	4
4	*Acanthurus achilles*	8.00	4
5	*Thalassoma duperrey*	6.44	4
6	*Pomacentrus jenkinsi*	5.25	4
7	*Acanthurus nigroris*	4.88	3
8	*Acanthurus leucopareius*	4.73	4
9	*Abudefduf sindonis*	3.64	4
10	*Chromis vanderbilti*	2.35	3

general appearance is one of bare rocks (Figure 4). Especially in the shallower regions, but decreasing with greater depths, this habitat is regularly swept by a strong surge. At depths varying with the relative proximity of a lee shore or protecting reef, but usually at about 12 to 17 m, the boulder habitat in many locations grades into the fields of fingerlike *Porites compressus*, one of the coral-rich habitats described above. Fishes listed in Table 3 [4] are characteristic of those seen in the boulder habitat during the day.

Shallow Reef-Flat Habitat

Shallow surge-swept reefs, the remains of ancient lava flows, extend offshore in several locations (Figure 5). Here, a solid pavement of exposed basalt, containing many cracks and crevices, supports a distinctive array of marine organisms. The predominant benthic life form is the coral

[4]Table 3 is based on data from four transects at four boulder sites—one at Cook Point, one at Mokuakae Bay, and two at Alahaka Bay (see Figure 1). Total number of species observed on these four transects: 77; mean number of individuals of all species for a single transect: 672.

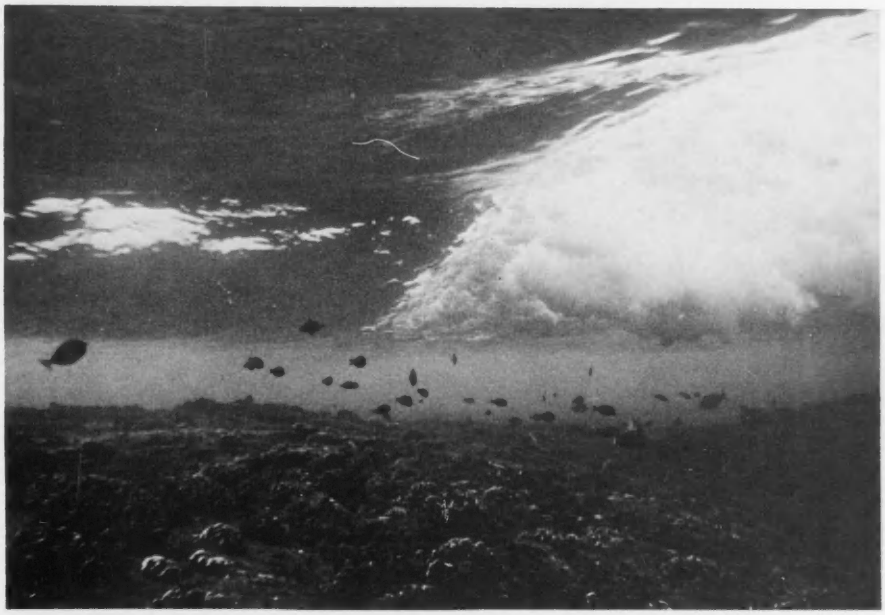

FIGURE 5.—Shallow reef-flat habitat. Most of the fishes shown are acanthurids, and include *Naso lituratus* and *N. unicornis*.

Pocillopora meandrina, growing as isolated heads 10 to 50 cm wide. The outstanding characteristics of this habitat, which generally has a maximum water depth of only about 3 to 4 m, are extreme water movement and wave shock. The fishes listed in Table 4 [5] are characteristic of those seen on shallow reef flats during the day.

[5]Table 4 is based on data from three transects at three shallow reef-flat sites at Palemano Point (see Figure 1). Note: one of the transect counts was aborted after 60 m when the surge became too strong to continue. Total number of species observed on these three transects: 54; mean number of individuals of all species for a single transect: 578.

TABLE 4.—The 10 fish species most frequently seen along transect lines in the shallow reef-flat habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 3$
1	*Acanthurus nigrofuscus*	20.23	3
2	*Thalassoma duperrey*	17.41	3
3	*Abudefduf imparipennis*	15.12	3
4	*Chromis vanderbilti*	10.33	3
5	*Thalassoma fuscus*	4.78	3
6	*Stethojulis balteata*	2.88	3
7	*Gomphosus varius*	2.78	3
8	Naso literatus	2.02	1
9	*Zebrasoma flavescens*	1.79	1
10	*Pomacentrus jenkinsi*	1.67	1

Reef-Face Habitat

At the offshore edge of the shallow reef flats, and at many locations along the shore, a sheer basalt face falls precipitously to water depths of 10 to 15 m (Figure 6). This situation produces a wide range of conditions within a limited area. In its upper regions the surge and wave shock are that of the reef-top habitat, but these rapidly abate with increasing depth. Conditions adjacent to the base of the reef face are essentially those of the boulder habitat, with fragmented pieces of the reef lying about as large boulders. The predominant forms of benthic life, dotting the rock surfaces, are *Pocillopora meandrina* (in the shallower regions), and smaller encrusting corals and algae. Many planktivorous fishes are concentrated in the water column adjacent to the reef face. Understandably, there is a greater variety of fishes in this habitat than in the other habitats characterized here. Fishes listed in Table 5 [6] are characteristic of those seen along the reef face during the day.

[6]Table 5 is based on data from three transects at two reef-face sites at Palemano Point (see Figure 1). Total number of species observed on these three transects: 89; mean number of individuals of all species for a single transect: 937.

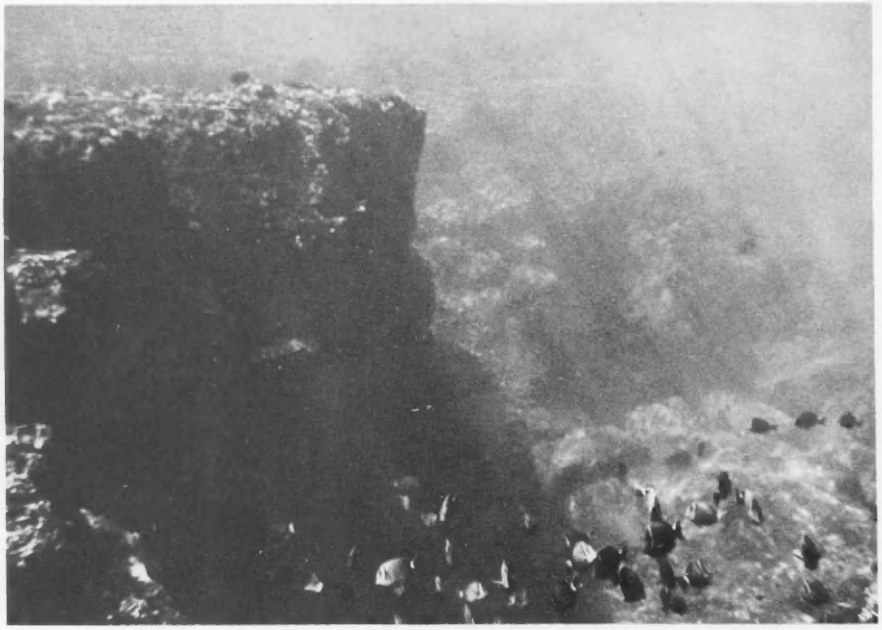

FIGURE 6.—Reef-face habitat. Most of the fishes shown swimming at the base of the reef are *Acanthurus leucopareius*. The reef face shown here drops 8 to 10 m.

TABLE 5.—The 10 fish species most frequently seen along transect lines in the reef-face habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 3$
1	*Chromis vanderbilti*	11.74	3
2	*Ctenochaetus strigosus*	9.54	3
3	*Zebrasoma flavescens*	9.11	3
4	*Acanthurus leucopareius*	7.18	3
5	*Acanthurus nigrofuscus*	6.17	3
6	*Thalassoma duperrey*	4.41	3
7	*Pomacentrus jenkinsi*	3.95	3
8	*Abudefduf abdominalis*	3.56	3
9	*Acanthurus achilles*	3.56	3
10	*Melichthys niger*	3.38	3

Outer Drop-Off Habitat

At the rim of the outer drop-off, 50 to 600 m from shore, where the sea floor falls abruptly from about 25 m to much greater depths, the sea floor generally is overgrown with the fingerlike form of *Porites compressus*, interspersed with massive heads of *P. pukoensis*, bare basalt boulders, and sand patches (Figure 7). The most striking characteristic of this habitat, aside from the spectacular way the sea floor falls away, is the large number of planktivorous fishes that abound in the water column. Obviously conditions for feeding on plankton are especially well developed here. The fishes listed in Table 6 [7] are characteristic of those seen on the rim of the outer drop-off during the day.

[7]Table 6 is based on data from four transects at four outer drop-off sites—two at Palemano Point and two at Puuhonua Point (see Figure 1). Total number of species observed on these four transects: 78; mean number of individuals of all species for a single transect: 478.

TABLE 6.—The 10 fish species most frequently seen along transect lines in the outer drop-off habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 4$
1	*Naso hexacanthus*	11.39	4
2	*Chromis leucurus*[1]	11.19	4
3	*Xanthichthys ringens*	10.50	4
4	*Thalassoma duperrey*	6.64	4
5	*Zebrasoma flavescens*	4.76	3
6	*Ctenochaetus strigosus*	3.87	2
7	*Chaetodon multicinctus*	3.76	3
8	*Centropyge potteri*	3.45	3
9	*Chromis verater*	3.24	2
10	*Pseudocheilinus evanidus*	2.40	2

[1]In making transect counts I followed Gosline and Brock (1960) in recognizing *Chromis leucurus* to include two color forms. Further study may show that two (or more) species are included here (see species account for *C. leucurus* in this report).

FIGURE 7.—Outer drop-off habitat. Most of the fishes shown in the water column are *Acanthurus thompsoni*.

Fishes Observed on Transect Lines

All fishes observed on transect lines in the five Kona habitats are listed in Table 7, where the value given for each species in each habitat is the relative abundance index, as defined in the methods. Transect data for each habitat category (number of transects, total number of species observed, and mean number of individuals on a single transect) are given in footnotes 2 to 7.

SPECIES ACCOUNTS

Family	*Page*
Muraenidae: moray eels	926
Congridae: conger eels	929
Synodontidae: lizardfishes	929
Brotulidae: brotulas	930
Atherinidae: silversides	931
Holocentridae: squirrelfishes	932
Aulostomidae: trumpetfishes	942
Fistulariidae: cornetfishes	944
Scorpaenidae: scorpionfishes	944
Serranidae: sea basses	947
Kuhliidae: aholeholes	948
Priacanthidae: bigeyes	948
Apogonidae: cardinalfishes	950
Carangidae: jacks	954
Lutjanidae: snappers	955
Sparidae: porgies	956
Mullidae: goatfishes	957
Kyphosidae: sea chubs	964
Chaetodontidae: angelfishes and butterflyfishes	964
Pomacentridae: damselfishes	978
Cirrhitidae: hawkfishes	986
Labridae: wrasses	989
Scaridae: parrotfishes	995
Blenniidae: combtooth blennies	998
Acanthuridae: surgeonfishes	1000
Zanclidae: moorish idol	1003
Bothidae: left-hand flounders	1005
Balistidae: triggerfishes	1005
Monacanthidae: filefishes	1009
Ostraciontidae: boxfishes	1011
Tetraodontidae: balloonfishes	1012
Canthigasteridae: sharp-backed puffers	1013
Diodontidae: spiny puffers	1015

This study treats only teleostean fishes, as these were almost the only kind observed on Kona reefs during this study. Elasmobranchs occurred infrequently and seemed to have little impact on the reef situation. No marine animals are more prominent than sharks in Hawaiian lore (e.g. Hobson and Chave, 1972), yet compared with most other tropical Pacific Islands, relatively few sharks are seen in Hawaiian nearshore waters today.

TABLE 7.—Relative abundance of fish species observed along transect lines in each of the Kona reef habitats.

Species	Coral-rich habitat Daytime	Coral-rich habitat Nighttime	Boulder habitat Daytime	Reef-flat habitat Daytime	Reef-face habitat Daytime	Outer Drop-off habitat Daytime
Superorder Elopomorpha:						
Order Anguilliformes:						
Family Muraenidae:						
Gymnothorax meleagris	—	—	0.04	0.06	—	—
Superorder Protacanthopterygii:						
Order Myctophiformes:						
Family Synodontidae:						
Synodus variegatus	0.04	—	—	—	—	—
Superorder Acanthopterygii:						
Order Beryciformes:						
Family Holocentridae:						
Holocentrus sammara	0.04	0.60	0.04	—	—	0.05
H. tiere	—	0.81	—	—	—	—
H. xantherythrus	—	0.60	—	—	—	—
H. diadema	—	1.01	—	—	—	0.05
H. lacteoguttatum	—	1.21	—	—	—	—
Holotrachys lima	—	0.81	—	—	—	—
Myripristis kuntee	0.23	23.61	0.19	—	0.43	0.26
M. murdjan	0.08	12.33	—	—	0.25	0.31
M. sp. (uncertain: either *M. murdjan* or *M. amaenus*)	—	5.24	—	—	—	—
Order Gasterosteiformes:						
Family Aulostomidae:						
Aulostomus chinensis	0.12	0.40	—	—	0.36	—
Family Fistulariidae:						
Fistularia petimba	—	—	—	0.12	—	—
Order Scorpaeniformes:						
Family Scorpaenidae:						
Taenianotus triacanthus	0.04	—	—	—	—	—
Scorpaena coniorta	—	0.20	—	—	—	—
Scorpaenopsis cacopsis	—	—	—	—	0.07	0.05
Order Perciformes:						
Family Serranidae:						
Cephalapholis argus	—	—	—	—	0.04	—
Family Priacanthidae:						
Priacanthus cruentatus	—	0.20	—	—	—	—
Family Apogonidae:						
Apogon menesemus	—	14.52	—	—	—	—
A. snyderi	—	11.90	—	—	—	—
Family Malacanthidae:						
Malacanthus hoedtii	—	—	—	—	—	0.16
Family Carangidae:						
Caranx melampygus	—	—	0.04	—	0.11	—
Family Lutjanidae:						
Aphareus furcatus	0.15	—	0.11	—	0.21	—
Family Sparidae:						
Monotaxis grandoculis	0.12	—	0.04	—	1.25	0.05
Family Mullidae:						
Mulloidichthys auriflamma	—	—	—	—	0.93	—
M. samoensis	0.12	—	—	—	0.14	—
Parupeneus multifasciatus	0.58	0.20	0.45	0.23	0.82	1.41
P. bifasciatus	0.12	—	0.07	—	0.71	0.05
P. chryserydros	0.27	—	0.15	—	0.25	—
P. porphyreus	0.08	—	—	—	—	—
P. pleurostigma	0.04	—	—	—	—	0.05
Family Kyphosidae:						
Kyphosus cinerascens	—	—	0.22	—	0.11	—
Family Chaetodontidae:						
Holacanthus arcuatus	—	—	—	—	0.11	0.10
Centropyge potteri	2.49	—	—	—	1.00	3.45
C. fisheri	—	—	—	—	—	0.16
Forcipiger flavissimus	0.96	—	1.01	0.35	0.78	1.41
F. longirostris	0.50	0.40	—	0.12	0.07	0.31
Hemitaurichthys thompsoni	—	0.40	—	—	—	0.73
H. zoster	—	—	0.26	—	—	2.09
Chaetodon corallicola	—	—	—	—	—	1.05
C. miliaris	—	—	—	—	—	1.05
C. quadrimaculatus	0.69	—	0.89	1.44	0.53	0.10
C. unimaculatus	—	—	0.22	1.21	—	—
C. multicinctus	4.41	4.03	1.08	0.58	0.82	3.76
C. ornatissimus	1.80	1.21	0.68	0.29	0.25	0.31
C. auriga	—	—	—	—	0.04	0.05
C. fremblii	0.08	0.20	0.30	0.12	0.32	0.05
C. lunula	0.69	1.21	0.15	0.40	2.03	0.58
C. lineolatus	—	0.20	0.11	—	0.11	—

TABLE 7.—Continued.

Species	Coral-rich habitat Daytime	Coral-rich habitat Nighttime	Boulder habitat Daytime	Reef-flat habitat Daytime	Reef-face habitat Daytime	Outer Drop-off habitat Daytime
C. reticulatus	—	—	—	0.12	—	—
C. trifasciatus	0.04	—	—	0.12	—	—
Family Pomacentridae:						
Plectroglyphidodon johnstonianus	3.07	0.20	0.07	1.04	0.25	1.25
Pomacentrus jenkinsi	6.71	—	5.25	1.67	3.95	0.68
Abudefduf sindonis	—	—	3.64	—	—	—
A. sordidus	—	—	0.22	—	0.39	—
A. imparipennis	—	—	0.22	15.12	—	—
A. abdominalis	0.35	0.20	—	—	3.56	—
Dascyllus albisella	0.19	1.21	0.07	—	—	2.30
Chromis vanderbilti	0.15	—	2.35	10.33	11.74	0.84
C. leucurus	12.30	—	—	—	0.82	11.19
C. verater	0.96	0.80	0.11	—	0.14	3.24
C. ovalis	0.11	0.40	—	—	—	—
Family Cirrhitidae:						
Paracirrhites arcatus	0.69	—	0.74	0.86	0.89	0.99
P. forsteri	0.23	—	—	0.12	0.11	—
Cirrhitops fasciatus	0.12	—	0.34	0.17	0.82	0.47
Cirrhitus pinnulatus	0.04	—	—	0.52	0.18	0.05
Family Labridae:						
Bodianus bilunulatus	—	—	—	—	—	0.05
Cheilinus rhodochrous	1.57	—	0.15	—	0.57	1.41
Pseudocheilinius octotaenia	1.30	—	0.07	—	0.82	1.93
P. tetrataenia	0.31	—	0.04	0.23	0.07	0.42
P. evanidus	0.04	—	—	—	—	2.40
Labroides phthirophagus	0.31	—	—	—	—	0.05
Thalassoma duperrey	5.71	—	6.44	17.41	4.41	6.64
T. fuscus	—	—	1.97	4.78	—	—
T. ballieui	0.04	—	0.15	0.17	0.21	0.05
T. lutescens	0.08	—	—	—	—	—
T. quinquevittata	—	—	—	0.23	—	—
Halichoeres ornatissimus	1.15	—	1.67	0.58	0.53	1.15
Stethojulis balteata	2.15	—	1.56	2.88	1.35	0.68
Anampses cuvier	0.08	—	0.34	0.06	0.07	0.05
Coris gaimard	0.81	—	0.26	0.35	0.71	1.31
C. flavovittata	—	—	—	—	0.04	—
C. venusta	—	—	—	—	0.11	—
Macropharyngodon geoffroy	0.15	—	0.07	0.52	0.21	0.73
Gomphosus varius	1.00	—	1.53	2.78	0.60	0.78
Cirrhilabrus jordani	—	—	—	—	—	0.16
Pseudojuloides cerasinus	—	—	—	—	—	0.05
Hemipteronotus taeniourus	—	—	—	—	—	0.16
Family Scaridae:						
Scarus sordidus	1.73	—	0.82	1.04	1.81	1.93
S. taeniurus	0.19	—	0.63	0.98	0.43	—
S. dubius	0.46	—	0.52	—	0.50	0.16
S. perspicillatus	0.35	0.20	1.53	—	0.28	0.10
S. rubroviolaceus	0.35	0.20	0.04	0.29	0.50	0.10
Calotomus spinidens	0.50	—	0.04	0.12	0.11	0.26
Unidentified juveniles	—	—	—	—	0.89	—
Family Blenniidae:						
Exallias brevis	0.15	—	0.11	0.06	0.11	0.05
Cirripectus obscurus	—	—	0.15	—	—	—
C. variolosus	0.31	—	0.04	—	0.07	—
Plagiotremus goslinei	—	—	0.19	0.98	0.04	—
P. ewaensis	—	—	—	—	0.04	—
Family Acanthuridae:						
Acanthurus achilles	0.69	1.41	8.00	0.35	3.56	0.10
A. dussumieri	0.35	—	0.74	—	0.28	—
A. glaucopareius	0.04	—	0.19	—	0.07	—
A. guttatus	—	—	1.64	—	—	—
A. leucopareius	0.69	1.01	4.73	0.40	7.18	—
A. nigrofuscus	4.37	0.40	13.74	20.23	6.17	1.62
A. nigroris	3.64	2.22	4.88	1.38	1.60	1.57
A. olivaceus	0.19	—	0.11	—	0.07	0.31
A. sandvicensis	0.12	2.40	1.64	0.12	0.71	—
A. thompsoni	—	—	—	—	—	1.88
A. xanthopterus	—	—	—	—	0.43	—
Ctenochaetus strigosus	15.45	—	10.77	—	9.54	3.87
C. hawaiiensis	0.58	—	0.82	—	0.75	0.05
Zebrasoma flavescens	10.58	6.85	9.61	1.79	9.11	4.76
Z. veliferum	0.15	—	0.22	—	—	—
Naso brevirostris	—	—	—	—	—	0.10
N. hexacanthus	—	—	—	—	1.28	11.39
N. lituratus	1.46	1.21	0.74	2.02	1.07	1.20
N. unicornis	0.35	—	0.60	1.50	0.25	0.05

TABLE 7.—Continued.

Species	Coral-rich habitat Daytime	Coral-rich habitat Nighttime	Boulder habitat Daytime	Reef-flat habitat Daytime	Reef-face habitat Daytime	Outer Drop-off habitat Daytime
Family Zanclidae:						
Zanclus canescens	0.38	—	1.38	1.21	0.82	1.10
Order Tetraodontiformes:						
Family Balistidae:						
Melichthys niger	1.00	—	0.82	0.12	3.38	—
M. vidua	0.04	—	—	—	—	0.15
Xanthichthys ringens	—	—	0.04	—	0.39	10.50
Rhinecanthus rectangulus	—	—	0.19	1.33	—	—
Sufflamen bursa	0.73	—	0.37	—	1.57	1.57
Balistid sp.	—	—	—	—	0.04	—
Family Monacanthidae:						
Cantherines dumerili	0.15	—	—	0.12	0.11	—
C. sandwichiensis	0.15	—	0.40	0.64	0.32	0.16
Pervagor spilosoma	0.35	—	—	—	0.04	0.10
P. melanocephalus	0.42	—	0.19	—	—	0.10
Alutera scripta	—	—	—	—	0.04	—
Family Ostraciontidae:						
Ostracion meleagris	0.19	—	0.86	0.12	0.18	—
Family Tetraodontidae:						
Arothron hispidus	—	—	—	—	0.04	—
A. meleagris	—	—	0.04	0.06	—	—
Family Canthigasteridae:						
Canthigaster amboinensis	0.12	—	0.22	0.17	0.11	—
C. jactator	0.46	—	0.04	—	0.78	0.05
C. coronatus	—	—	—	—	0.04	0.10

The observations for each species are grouped by order and family in phylogenetic sequence, as listed by Greenwood et al. (1966). Species names generally are those used by Gosline and Brock (1960), except where more recent taxonomic studies indicate change. All sizes given are standard length. For most species, the number of specimens collected is followed by, in parenthesis, their mean size and the range in their sizes. All species accounts consider individuals showing morphology and behavior of adults.

ORDER ANGUILLIFORMES

Family Muraenidae: moray eels

Most Hawaiian eels belong to this family, which comprises the moray eels, or *puhi,* as Hawaiians call them (Gosline and Brock, 1960). Morays are denizens of crevices in the reefs, and because most remain secreted under cover, their great abundance cannot be appreciated by a casual observer. Nevertheless, the morays include more species (32 reported) on Hawaiian reefs than any other family of fishes, except perhaps the wrasse family Labridae (Gosline and Brock, 1960). Most Hawaiian morays do not grow to more than about 60 cm long, although a few may attain a length of about 2 m (Gosline and Brock, 1960). Most of them remain secreted in reef crevices, but the five species considered below are examples of those that are often exposed on the reef top.

Gymnothorax meleagris (Shaw and Nodder) —spotted moray, *puhi 'oni'o*

This medium-sized eel characteristically protrudes its head from crevices during the day (Figure 8), and thus is the moray most often in view on the reef; however, I seldom saw it after dark. Of the nine specimens collected, the stomachs of five were empty, although three of these contained unidentified fragments at the posterior end of their intestines. Of the four with prey in their stomachs, one (455 mm) taken during midmorning contained a fresh damselfish, *Abudefduf imparipennis* (40 mm) that appeared to have been recently captured. Two others with full stomachs were collected during late afternoon: one (321 mm) contained a moderately digested xanthid crab, whereas the other (121 mm) contained a well-digested fish. On the other hand, the fourth specimen (361 mm) contained a moderately digested xanthid crab that appeared to have been in the eel's stomach at least several hours when it was collected during morning twilight.

CONCLUSION.—*Gymnothorax meleagris* captures small fishes and crustaceans by day and probably also at night.

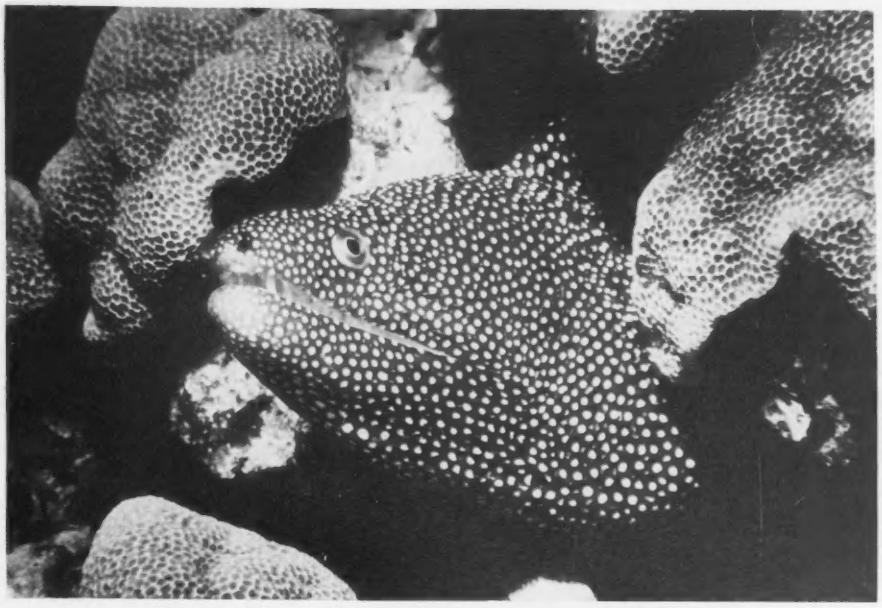

FIGURE 8.—*Gymnothorax meleagris*, a moray eel, showing daytime attitude.

***Gymnothorax eurostus* (Abbott)**

This small species, which attains a maximum length of about 60 cm, is probably the most numerous moray in Hawaii (Gosline and Brock, 1960). However, it is a secretive species, only occasionally visible on the reef. Although the four individuals collected (360: 294-432 mm) were speared as they protruded their heads from holes in the reef during the day, this habit is not characteristic of *G. eurostus*, as it is of *G. meleagris*, above. Two of those collected had empty stomachs, but the other two, both taken during midday, contained relatively fresh prey—a caridean shrimp in one, a xanthid crab in the other.

CONCLUSION.—*Gymnothorax eurostus* captures crustaceans during the day. The nighttime situation remains uncertain.

Gymnothorax flavimarginata* (Rüppell)—*puhi paka

This eel, which attains a length of about 120 cm (Gosline and Brock, 1960), is the most numerous of the larger muraenids in Kona. Being so abundant, as well as large, this heavy-bodied eel probably represents the greatest threat among morays to humans. It is the species that most often appears when a fish has been speared during daylight. The regularity and promptness of these appearances make it clear that *G. flavimarginata* is especially sensitive to fish that are injured, or perhaps otherwise under stress. In this respect it is similar to *G. castaneus* in the Gulf of California (Hobson, 1968a). Usually when a reef fish is injured, or seriously threatened, it takes cover in a reef crevice. Usually such individuals are to some extent incapacitated, and thus vulnerable to predators equipped to seek them out. Probably *G. flavimarginata* is adapted to this task. Other large morays on the reef show the same behavior, but to a lesser degree. Most encounters with *G. flavimarginata* were by day; although its behavior would seem equally adaptive to nocturnal conditions, it was only occasionally observed after dark.

CONCLUSION.—*Gymnothorax flavimarginata* is especially sensitive to stimuli emanating from a fish in distress, and appears adapted to seeking out such individuals when they have sought shelter in reef crevices.

Gymnothorax petelli (Bleeker)—broad-banded moray

The broad-banded moray generally is out of sight within the reef during daylight, but often active in exposed locations after dark (Figure 9). A second species, *G. undulatus*, similarly forays away from cover at night, but during this study was seen less often than *G. petelli*. Although no specimens were examined, one *G. petelli* seen on the reef at night was grasping between its jaws a pufferfish, *Canthigaster jactator*. Additional evidence of nocturnal habits in *G. petelli* was given by Chave and Randall (1971), who described it pursuing crabs over underwater sand patches at night.

CONCLUSION.—*Gymnothorax petelli* is a nocturnal predator.

Echidna zebra (Shaw)—zebra moray

The zebra moray has a blunter snout than the species of *Gymnothorax* treated above, but its dentition is even more distinctive. Morays of the genus *Gymnothorax* have fanglike teeth that are suited to grasping prey, but the zebra moray, like other species of the genus *Echidna*, has blunt, pebblelike teeth that are suited to crushing prey. Gut contents are consistent with this observation: all four specimens (750: 485-835 mm) taken at various times of the day contained the crushed remains of relatively large crabs—considerably larger than crabs found in comparably sized individuals of *Gymnothorax*. The zebra moray is a sluggish animal, even for a moray, and is generally secretive. Usually all one sees of this animal, day or night, is a motionless segment of its body, visible at a narrow opening in the reef.

CONCLUSION.—*Echidna zebra* captures crustaceans within reef crevices, taking larger individuals of the more heavily armored prey than do species of *Gymnothorax*.

General Remarks on Moray Eels

Morays have been widely considered, collectively, as nocturnal animals (e.g. Winn and Bardach, 1959; Starck and Davis, 1966; Randall,

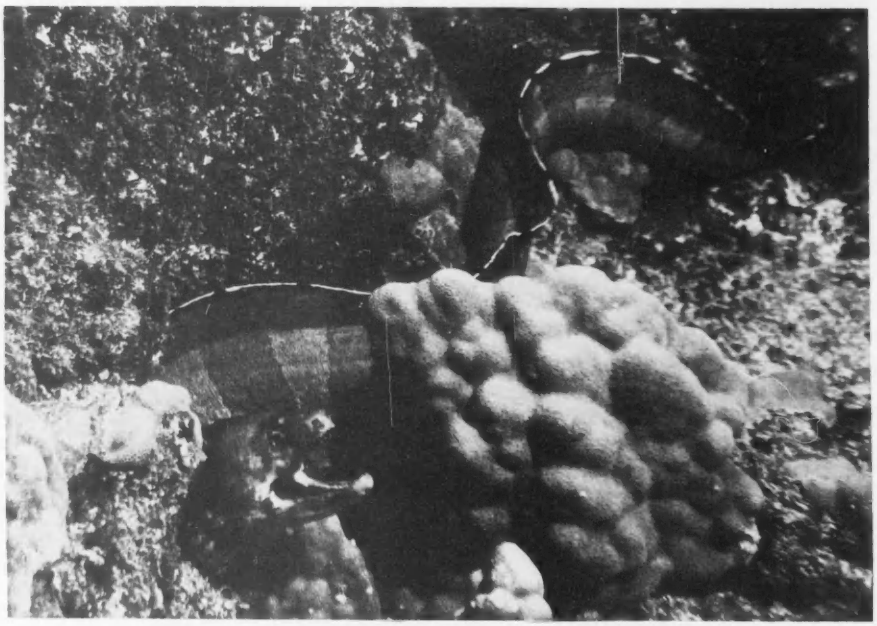

FIGURE 9.—*Gymnothorax petelli*, a moray eel, on the reef top at night.

1967; Collette and Talbot, 1972). Hiatt and Strasburg (1960) attributed the high incidence of empty stomachs in morays from the Marshall Islands during daylight to nocturnal habits; however, I concur with Gosline and Brock (1960), who attributed the empty stomachs of Hawaiian morays during the day to infrequent feeding, rather than necessarily to nocturnal feeding. Certainly some morays seem to be primarily nocturnal—*Gymnothorax petelli* and *G. undulatus*, described above, are examples. But others described here, such as *G. meleagris*, *G. eurostus*, and *G. flavimarginata*, feed regularly in daylight. That some morays are primarily diurnal was illustrated by Chave and Randall (1971), who described a diurnally active, nocturnally inactive pattern for *G. pictus* in the central Pacific. Conclusions on relative activity between day and night for moray eels remain tenuous if based solely on how often, and at what time, the species is seen in exposed positions. Moray eels are adapted to activity within reef crevices, and one would expect at least most of them to best capture their prey there; indeed, most species rarely expose themselves, day or night.

Family Congridae: conger eels

Conger marginatus* Valenciennes—white eel, *puhi uha

The white eel, which may exceed a length of 1 m (Gosline and Brock, 1960), is relatively numerous in Kona. It moves about in the open on the reef after dark and rests in reef crevices during daylight. In the Marshall Islands, Hiatt and Strasburg (1960) reported similar behavior in *C. noordzieki*, which preys on both fishes and invertebrates.

CONCLUSION.—*Conger marginatus* is active in exposed locations on the reef after dark.

Order Myctophiformes

Family Synodontidae: lizardfishes

Saurida gracilis* (Quoy and Gaimard)–*'ulae nihoa

Attaining lengths of over 300 mm, this is the largest of those lizardfishes that are numerous on the reef. During both day and night it rests motionless and fully exposed on sand patches, rock, or coral. Despite these exposed positions, it is difficult to detect, so closely does its coloration match the surroundings. Six specimens (223: 165-315 mm) were examined. The guts were empty in five—four speared at night, between 2300 h and dawn, and one taken during midday. The sixth specimen (165 mm), taken 1 h before midnight, contained the well-digested anterior half of a trumpetfish, *Aulostomus chinensis* (about 90 mm when intact). Because digestion was far advanced, this prey may have been ingested during the previous day or evening twilight. These limited data suggest that attacks are infrequent, or perhaps that feeding habits are diurnal or crepuscular. Hiatt and Strasburg (1960) reported strictly piscivorous habits for this species in the Marshall Islands, and described daylight attacks in which it darted upward from a resting spot on the sea floor.

CONCLUSION.—*Saurida gracilis* attacks small fishes in daylight.

Synodus variegatus* (Lacépède)—*'ulae 'ula

This is the most numerous synodontid on Kona reefs. During both day and night it rests on the sea floor (Figure 10), as does *Saurida gracilis*, above. Although usually in exposed positions, it is difficult to detect because its coloration closely matches the background. Frequently it becomes even more inconspicuous by burying in the sand, leaving only its eyes and the tip of its snout exposed.

Once, during early afternoon, an individual of this species shot up from the coral and captured a small wrasse, *Thalassoma lutescens*, that I was stalking. The wrasse was watching me when the lizardfish struck, and the attacker may have sensed this distraction in its prey. I speared the predator immediately after the attack, and found it to be 166 mm long (it lost the wrasse when speared and is included below among those with an empty gut). Two other noteworthy incidents occurred at night: On both occasions I was hunting specimens among the coral, and my spear, projecting into my path, was faintly illuminated by my companion's diving light. Suddenly, an individual of this species darted up and struck the silver barb on the otherwise grey spear. Although the nearby diving light created here an unnatural nocturnal situation, these two fish obviously were alert for prey at these times.

Twelve specimens (142: 94-158 mm) were collected during day and night from exposed posi-

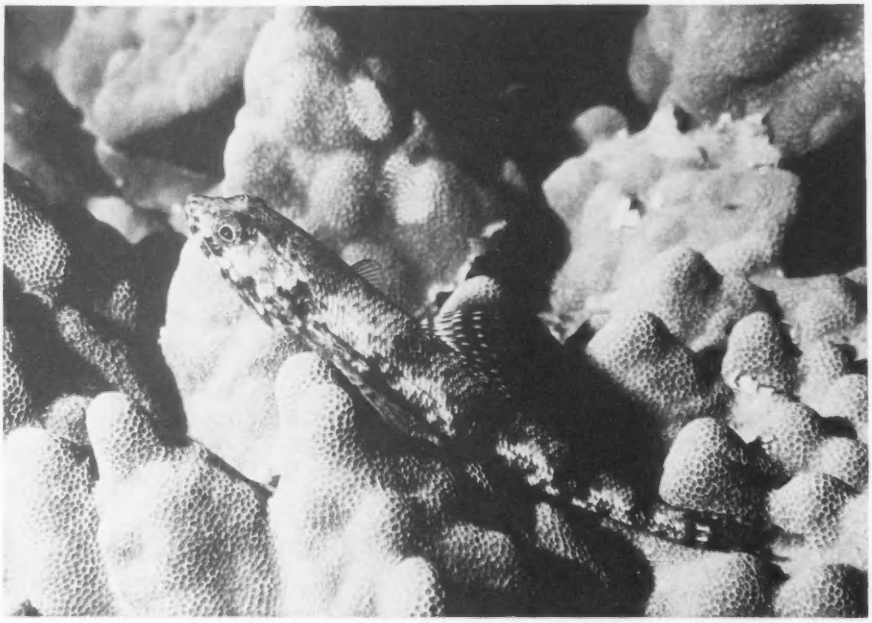

FIGURE 10.—*Synodus variegatus*, a lizardfish, poised to strike at prey in the water overhead.

tions on the sea floor. Of nine speared during afternoons, six had empty guts, but two contained fish fragments, and one contained three fish—two digested beyond recognition, and one relatively fresh *Plagiotremus goslinei* (32 mm). Of two collected during morning twilight, one was empty, while the other contained an extensively digested fish (25 mm). Finally, one collected at night, 5 h after sunset, contained fish fragments.

CONCLUSION.—*Synodus variegatus* attacks small fishes during the day and probably also at night.

General Remarks on Lizardfishes

Similar behavior is widely reported for the synodontids of tropical seas. In the Florida Keys, Starck and Davis (1966) reported that *Synodus synodus* and *Trachinocephalus myops* lie partially buried in the sand and erupt to capture prey swimming overhead during the day. Similarly, Randall (1967) noted that lizardfishes in the West Indies, including *S. synodus*, *S. intermedius*, and *S. foetens*, may rest on rocks, sand, or mud, where they sometimes partially bury themselves. Hartline et al. (1972) observed on several occasions during the day *Synodus* sp. in the Virgin Islands attacking the damselfish *Chromis cyaneus* from resting positions on the substratum. Similar observations were also reported by Smith and Tyler (1972). Although fishes seem to be the major prey of synodontids, Randall (1967) found some shrimps and squids in the predominantly piscivorous diet of lizardfishes in the West Indies. Suyehiro (1942) also reported shrimps and squid secondary prey to fishes in the diet of *Saurida undosquamis* in Japan. Probably any free-swimming animal of appropriate size becomes prey if it passes close above a waiting lizardfish when conditions are suitable for attack. The jaws of lizardfishes are profusely rimmed with sharp, inwardly depressible canine teeth, like those of many morays, and this type of dentition is especially well suited to grasping small fishes.

ORDER GADIFORMES

Family Brotulidae: brotulas

Brotula multibarbata Temminck and Schlegel—*puhi palahoana*

This fish is not in view during daylight, except to one who enters some of the darker caves. Although diurnally secretive, it swims into the open

on the reef after dark, but even then is mostly exposed only during transit from one crevice to another.

Seven individuals (169: 73-250 mm) were speared during day and night. Two collected about 2 h before daybreak as they swam close among rocks were both full of prey, including fresh material. Of three others collected in dark caves during midmorning, one was empty and the other two contained only well-digested fragments. Finally, two individuals collected within 1 h after nightfall as they swam in exposed locations among rocks were both empty—apparently having not yet captured prey on their nocturnal foray. The four individuals containing identifiable prey had fed on the items listed in Table 8.

CONCLUSION.—*Brotula multibarbata* is a nocturnal predator that feeds mostly on crustaceans and fishes.

General Remarks on Brotulas

Hiatt and Strasburg (1960) concluded that *Dinematichthys ilucoeteoides* in the Marshall Islands is very secretive because they never saw a live one, but did not suggest that it might be nocturnal. They believed that by concealing itself in crevices this brotulid is able to dash out and capture small fishes and crustaceans that unsuspectingly venture close to its hiding place. Starck and Davis (1966) recognized nocturnal habits in an Atlantic species, *Petrotyx sanguineus*, which is unseen in daylight, but swims close among reef ledges at night.

Order Atheriniformes

Family Atherinidae: silversides

Pranesus insularum (Jordan and Evermann)—*'iao*

This silverside is not numerous in Kona, but in daylight small schools of relatively inactive individuals occur at various places along the rocky shore, right at the water's edge. At nightfall these schools disperse, and the members move away from shore, over the reef. They swim high in the water column, just under the water surface, and some of them range out at least as far as the offshore drop-off.

Using a hard net, 13 individuals (47: 39-70 mm) were collected during both dark nights and moonlit nights—9 between 4 and 6 h after sunset and 4 during the 2 h before first morning light. Although the gut of 1 was empty, the other 12 were full, including fresh material, as listed in Table 9.

CONCLUSION.—*Pranesus insularum* is a nocturnal planktivore that takes mostly crustaceans and foraminiferans.

Table 8.—Food of *Brotula multibarbata*.

Rank	Items	No. fish with this item (n = 4)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	1	25.0	6.25
2	Fish	1	16.3	4.08
3	Decapod shrimps	1	6.3	1.58
4	Mysids	1	5.0	1.25
5	Crab megalops	1	0.3	0.08
Also, crustacean fragments		2	37.5	18.75
	Unidentified fragments	3	9.6	7.20

Table 9.—Food of *Pranesus insularum*.

Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Mysids	5	14.2	5.92
2	Decapod shrimp larvae	5	6.7	2.79
3	Foraminiferans	4	6.3	2.10
4	Calanoid copepods	2	4.2	0.70
5	Larvaceans	1	2.1	0.18
6	Crab zoea	1	1.7	0.14
7	Spider	1	0.4	0.03
Also, crustacean fragments		12	40.8	40.80
	Unidentified fragments	7	23.6	13.79

General Remarks on Silversides

It is widely recognized that silversides prey largely on zooplankton. Hiatt and Strasburg (1960) found mostly zooplankton in three species in the Marshall Islands, as did Randall (1967) in two species from the West Indies. Each report listed shrimp larvae and copepods among the major food items, but neither mentioned nocturnal habits. At Majuro Atoll, Marshall Islands, *Pranesus pinguis* is inactive in schools along lagoon beaches during the day, and then migrates offshore into the lagoon at nightfall, where it disperses and feeds on zooplankton in the surface waters (Hobson and Chess, 1973). The closely related *P. insularum* does not move so far from shore at night in Kona, presumably because its feeding grounds are over the nearshore reefs.

Order Beryciformes

Family Holocentridae: squirrelfishes

The squirrelfishes compose one of the more prominent groups of fishes on Hawaiian reefs. The species fall into two major categories: those in one group include members of the genus *Holocentrus*, which are known by the generic Hawaiian name *ala 'ihi*, and one species of the genus *Holotrachys*; those in the second group include species of the genus *Myripristis*, which are known by the generic Hawaiian name *'u'u*, or perhaps more often today by the Japanese equivalent *menpachi*.

Holocentrus sammara (Forskål)

This solitary fish is numerous in coral-rich surroundings at depths between 4 and 20 m. It is a relatively large species—up to 300 mm long (Gosline and Brock, 1960)—and characteristically hovers in visible locations at the openings of reef caves during the day. During evening twilight it moves away from its daytime shelter-sites and throughout the night ranges over the nearby areas of the reef, staying close to the sea floor. During morning twilight it gradually moves closer to cover and by sunrise has resumed its daytime mode of behavior. After dark the coloration of this fish differs from its coloration in daylight (Figure 11a and b).

Twenty-one specimens (162: 128-202 mm) were collected during day and night for food-habit study. All 13 that were speared as they swam in exposed positions on the reef during the last hours of darkness, before daybreak, and during morning twilight contained prey in varying stages of digestion. In comparison, of seven speared as they hovered close among coral shelter during the afternoon, four were empty, two contained only well-digested fragments, and one contained an apparently recently ingested crab. Finally, one that was speared in the open 4 h after nightfall was full of prey, most of it fresh. Items in the 17 specimens containing identifiable material are listed in Table 10.

CONCLUSION.—*Holocentrus sammara* is a nocturnal predator that feeds mostly on benthic crustaceans, especially xanthid crabs and caridean shrimps, but some feed diurnally.

Holocentrus spinifera (Forskål)

This is the largest squirrelfish on Kona reefs, and of those considered in this report it is also the least numerous. A solitary species during both day and night, it is secretive within reef crevices in daylight, but ranges out and forages close to the reef after dark. In daylight, the body of this fish is a plain rosy-red, and its dorsal fin is yellow; in darkness, however, a small but prominent white spot appears on each side of its body, just behind its dorsal fin. Because this large fish is not numerous, I came to recognize certain individuals and found that after nocturnal forays on the reef each tended to return each morning to its particular shelter spot.

Six specimens (213: 68-350 mm) were speared during day and night for study of food habits. The one that was taken during midday contained a large caridean shrimp, *Saron marmoratus* (about 40 mm), that was extensively damaged by digestion and could have been taken during the previous night. A second, taken as it emerged from cover at nightfall, was the only one taken with an empty gut. Of the other four, all of which contained relatively fresh prey, three were collected as they swam in the open at night, more than 3 h after sunset, and the fourth was collected under a ledge during morning twilight.

All five specimens containing food had fed on crustaceans exclusively. Three had taken caridean shrimps (mean percent of diet volume: 34; ranking index: 20.4), three had taken xanthid crabs (mean percent of diet volume: 31; ranking index: 18.6), and one had taken a scyllarid lobster (mean percent of diet volume: 11; ranking index:

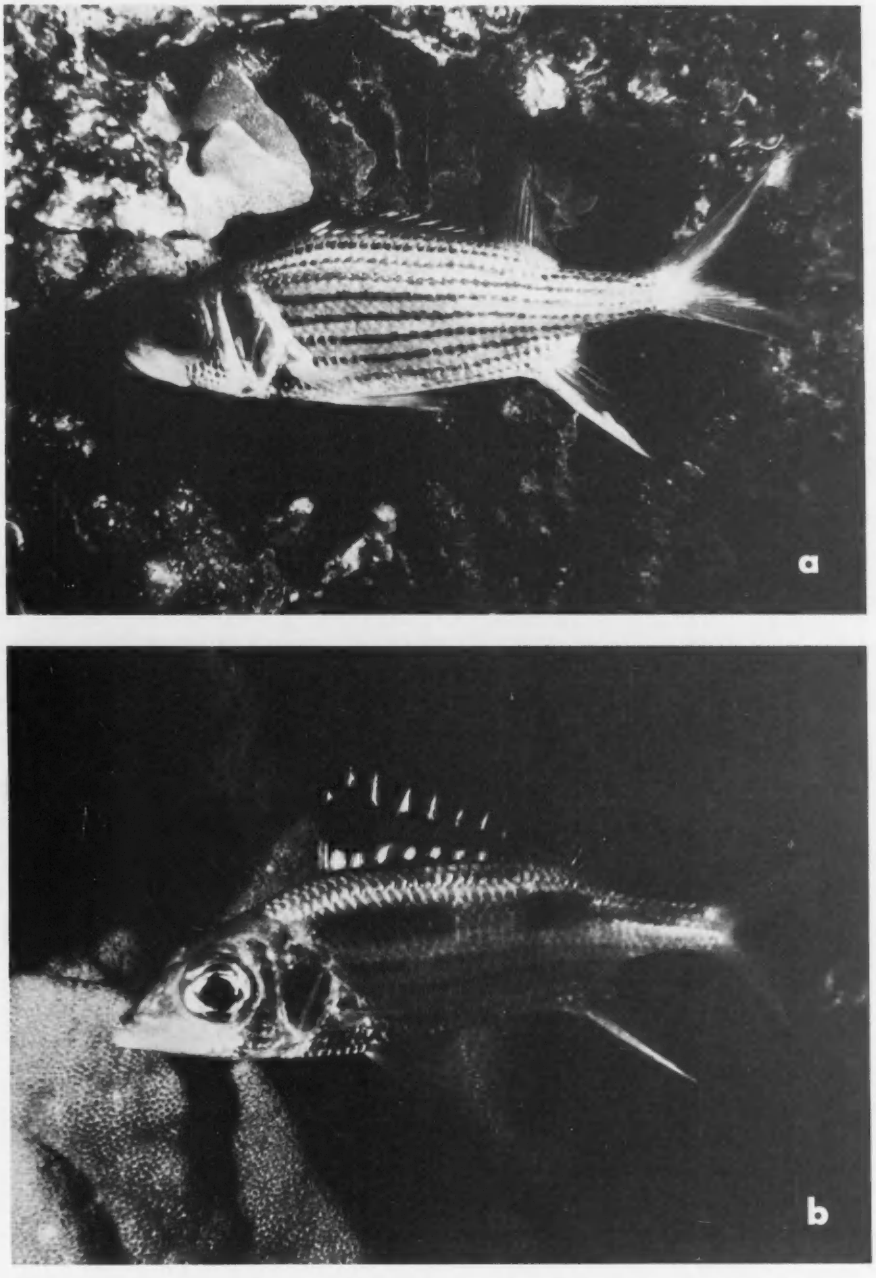

FIGURE 11.—*Holocentrus sammara*, a squirrelfish: a, showing its diurnal coloration under a ledge during the day; b, showing nocturnal coloration as it swims close to the reef at night.

TABLE 10.—Food of *Holocentrus sammara*.

Rank	Items	No. fish with this item (n = 17)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	12	52.5	37.08
2	Caridean shrimps	4	12.2	2.88
3	Portunid crabs	2	7.8	0.92
4	Fish	2	7.8	0.92
5	Penaeid shrimps	1	5.9	0.35
Also, crustacean fragments		4	13.8	3.25

2.2). Three contained unidentified crustacean fragments (mean percent of diet volume: 24; ranking index: 14.4).

CONCLUSION.—*Holocentrus spinifera* is a nocturnal predator that feeds mostly on benthic crustaceans, especially caridean shrimps and xanthid crabs.

Holocentrus tiere Cuvier

This relatively numerous holocentrid is mostly secreted in reef caves during the day, but after dark swims in exposed locations at depths below 5 m, especially along reef ledges. It emerges from cover after last evening light and regains shelter before, or at, first morning light. Like *H. sammara* and *H. spinifera*, above, *H. tiere* has distinctive diurnal and nocturnal color patterns (Figure 12a and b).

Fifteen specimens (141: 67-160 mm) were speared as they swam in the open at night, or just after they had returned to shelter at daybreak: 11 of these had food in their stomachs; 3 taken within 4 h after sunset were empty—apparently their nocturnal hunt had not yet been successful; 1 taken under a ledge during morning twilight also had an empty gut, indicating that it had passed the night without feeding. Items in the 11 specimens containing identifiable material are listed in Table 11.

CONCLUSION.—*Holocentrus tiere* is a nocturnal predator that feeds mostly on benthic crustaceans, especially xanthid crabs and caridean shrimps.

Holocentrus xantherythrus Jordan and Evermann

During the day this relatively small holocentrid aggregates in crevices and under overhangs of basalt reefs (Figure 13) in water deeper than 6 m, but especially below 20 m. After dark it ranges out from this shelter and into the surrounding areas, where solitary individuals are active close to rock, coral, or pockets of sand. By first morning light it has returned to its daytime retreats. At night this fish has prominent white vertical markings on its body like those illustrated for *H. tiere* (Figure 12b).

Of the 29 individuals (106: 88-123 mm) speared at different times of day and night, the stomachs of all 15 that were active in exposed locations on the reef during the 2 h immediately before daybreak, or were under reef shelter within an hour of sunrise, contained prey in varying stages of digestion, whereas the stomachs of all 11 taken from reef crevices during afternoons were empty. The remaining three were taken within 2 h after last light, shortly after they had begun their nightly foraging, and although one was empty, the other two contained fresh prey. Items in the 17 specimens that contained identifiable material are listed in Table 12.

CONCLUSION.—*Holocentrus xantherythrus* is a nocturnal predator that feeds mostly on benthic crustaceans, although some free-swimming crustaceans are also taken close to the bottom.

Holocentrus diadema Lacépède

After dark, many individuals of this relatively small squirrelfish swim close to the sea floor where coral growth is rich at depths below 3 to 4 m. *Holocentrus diadema* is secretive by day, generally remaining out of sight within the many narrow interstices of its coral-rich habitat, but is occasionally glimpsed in the shadows at the base of coral heads. Generally, it does not leave its daytime shelter until after last evening light, and returns to cover before or at first morning light. At night this fish, like *H. xantherythrus*, above, has prominent white vertical markings on its body that are similar to those on the nocturnally active *H. tiere* (Figure 12b).

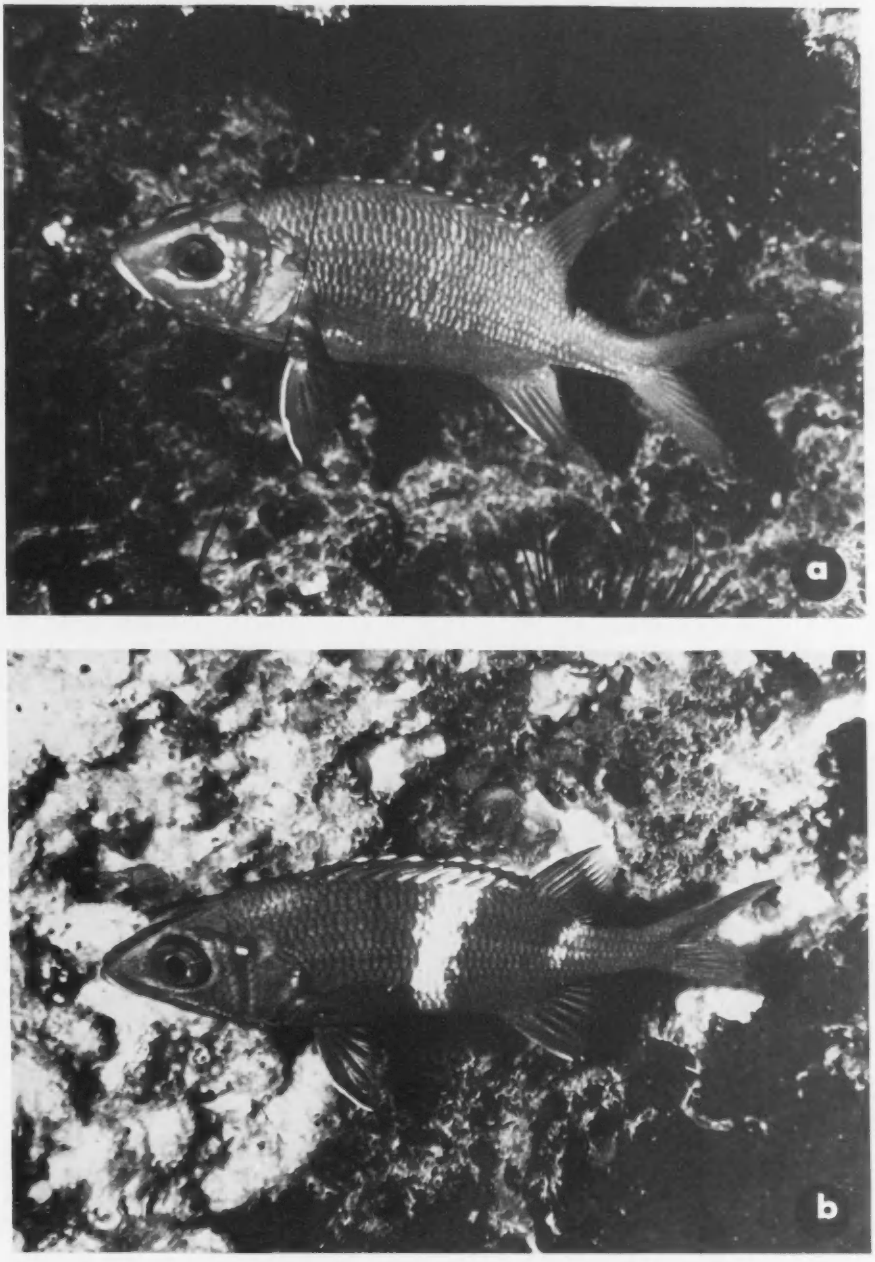

FIGURE 12.—*Holocentrus tiere*, a squirrelfish: a, showing diurnal coloration under a ledge during the day; b, showing nocturnal coloration as it swims close to the reef at night.

TABLE 11.—Food of *Holocentrus tiere*.

Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	8	38.7	28.15
2	Caridean shrimps	5	24.7	11.23
3	Crab megalops	5	4.8	2.18
4	Fish	1	1.8	0.16
5	Polychaetes	1	0.2	0.02
6	Sipunculid introverts	1	0.1	<0.01
Also, crustacean fragments		8	29.7	21.60

TABLE 12.—Food of *Holocentrus xantherythrus*.

Rank	Items	No. fish with this item (n = 17)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	12	42.3	29.86
2	Crab megalops	11	14.8	9.58
3	Caridean shrimps	7	15.1	6.22
4	Prosobranch gastropods	4	2.3	0.54
5	Stomatopods	2	1.9	0.22
6	Opisthobranch gastropods	1	0.9	0.05
7	Sipunculid introverts	1	0.8	0.05
8	Pelecypods	1	0.6	0.04
9	Euphausiids	1	0.3	0.02
10	Oxyrhynchid crabs	1	0.3	0.02
11	Tanaids	2	0.2	0.02
12	Flabelliferan isopods	1	0.1	0.01
13	Mysids	1	0.1	0.01
Also, crustacean fragments		10	20.3	11.94

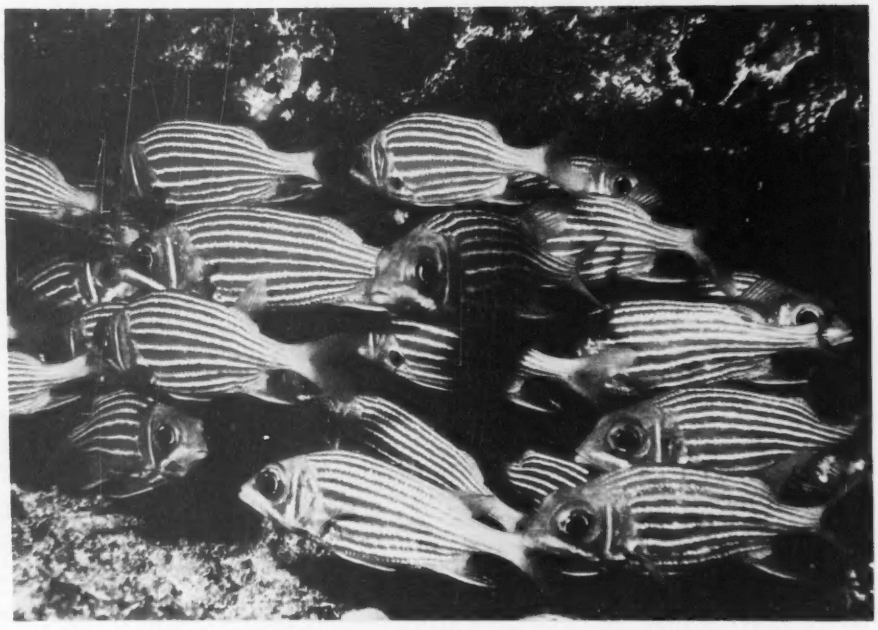

FIGURE 13.—*Holocentrus xantherythrus*, a squirrelfish, aggregated under a ledge during the day.

TABLE 13.—Food of *Holocentrus diadema*.

Rank	Items	No. fish with this item (n = 26)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	17	26.7	17.46
2	Ophiuroids	12	12.0	5.54
3	Crab megalops	11	12.4	5.25
4	Caridean shrimps	11	9.7	4.10
5	Prosobranch gastropods	13	6.2	3.10
6	Polychaetes	6	6.1	1.41
7	Gammaridean amphipods	5	1.7	0.33
8	Penaeid shrimps	2	2.3	0.18
9	Isopods	3	1.4	0.16
10	Chitons	1	1.7	0.07
11	Mysids	2	0.8	0.06
12	Portunid crabs	1	0.8	0.03
13	Holothurians	1	0.6	0.02
14	Oxyrhynchid crabs	1	0.4	0.02
15	Tanaids	1	0.4	0.02
16	Calanoid copepods	1	0.4	0.02
17	Pelecypods	1	0.4	0.02
18	Opisthobranch gastropods	1	0.2	0.01
19	Echinoids	1	0.2	0.01
20	Harpacticoid copepods	1	0.1	<0.01
21	Limpets	1	0.1	<0.01
Also, crustacean fragments		15	11.3	6.63
	Unidentified fragments	4	3.9	0.60

Twenty-eight specimens (109: 85-127 mm) were speared as they swam in exposed locations on the reef at various times during the night. Only two had empty stomachs: in one of these, taken shortly after nightfall, the entire gut was empty, which indicated it had not as yet hunted successfully that night; the other, taken with an empty stomach just before daybreak, had a full intestine, suggesting that it had fed early but not late during the night. The other 26 specimens all contained food in varying stages of digestion, most of it identifiable, as listed in Table 13.

CONCLUSION.—*Holocentrus diadema* is a nocturnal predator that feeds mostly on benthic crustaceans, although it also takes free-swimming forms close to the bottom.

Holocentrus lacteoguttatum Cuvier

This small squirrelfish is similar to *H. xantherythrus* and *H. diadema*, but frequents shallower water than the other two, being most numerous during the day in rocky crevices along surge-swept shores, often where the water is only 1 to 4 m deep. It aggregates in these crevices, and after nightfall ranges out over coral, rock, or pockets of sand on the surrounding reef. Gosline and Brock (1960) also noted the shallowwater habits of this species, but in at least some situations it occurs in depths below 30 m (Gosline, 1965). These habitat distinctions are clearest in daylight, when the three species have retired to their shelters. The differences are less clear at night, when their activity ranges overlap. *Holocentrus lacteoguttatum* does not seem to have prominent nocturnal color features, as do certain other species of *Holocentrus*, treated above; however, several individuals after having been speared at night showed faint traces of essentially the same white markings characteristic of nocturnally active individuals of *H. xantherythrus*, *H. diadema*, and *H. tiere* (see Figure 12b).

Twenty-one specimens (88: 52-104 mm) were collected at various times of day and night. All but 1 of 13 active individuals that were speared in the open at night (more than 4 h after sunset and before they had returned to shelter at daybreak) had food in their stomachs; the lone exception, collected 4 h after sunset, had a completely empty gut, indicating it had not yet hunted successfully that night. In comparison, only one of five collected from aggregations under shelter during midmorning had material in its stomach, and this was extensively digested (all had full intestines, however). Finally, all three that were collected from aggregations under shelter during late afternoon had completely empty guts, except for a few well-digested fragments posteriorly. Items in the 13 specimens containing identifiable material are listed in Table 14.

TABLE 14.—Food of *Holocentrus lacteoguttatum*.

Rank	Items	No. fish with this item (n = 13)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	13	36.3	36.30
2	Crab megalops	9	8.0	5.54
3	Gammaridean amphipods	8	5.1	3.14
4	Tanaids	6	3.7	1.71
5	Polychaetes	4	4.9	1.51
6	Caridean shrimps	3	1.9	0.44
7	Harpacticoid copepods	3	0.8	0.19
8	Echinoids	3	0.8	0.19
9	Sipunculid introverts	1	1.8	0.14
10	Prosobranch gastropods	1	1.0	0.08
11	Oxyrhynchid crabs	1	0.3	0.02
12	Calanoid copepods	1	0.3	0.02
13	Limpets	1	0.2	0.02
14	Ophiuroids	1	0.1	0.01
Also, crustacean fragments		13	28.1	28.10
	Unidentified fragments	4	6.7	2.06

CONCLUSION.—*Holocentrus lacteoguttatum* is a nocturnal predator that feeds primarily on benthic crustaceans, although some free-swimming forms close to the bottom are also taken.

Holotrachys lima (Valenciennes)

This fish is secreted far back in reef crevices during daylight. After dark, however, solitary individuals are widespread in exposed positions, swimming even closer to the reef than do the species of *Holocentrus*, discussed above. Unlike the others, which often swim over sand patches, this species stays over rock or coral. It did not display distinctive day or night color features, being at all times a solid rose-red.

Twenty specimens (91: 70-113 mm) were collected during day and night. Thirteen were active in exposed positions on the reef at night when speared, and the stomachs of eight contained prey, much of it fresh. Of the five taken after dark with empty stomachs, the entire gut was empty in three collected before midnight, indicating they had not yet hunted successfully that night; however, the gut was also empty in one speared just before dawn, indicating it had passed the entire night without feeding; the fifth individual with an empty stomach also was collected just before dawn, but its intestine was full, indicating that it probably had fed earlier during the night. Six of seven specimens collected from deep crevices during late morning had empty stomachs, and the extensively damaged material in the seventh individual probably had been ingested during the previous night. (Rotenone was used to collect this species during the day, a departure from the standard collecting method that was necessary because this secretive fish is only rarely seen in daylight.) Items in the 10 specimens containing identifiable material are listed in Table 15.

CONCLUSION.—*Holotrachys lima* is a nocturnal predator that feeds mostly on benthic crustaceans, although some free-swimming forms close to the bottom also are taken.

Myripristis kuntee Cuvier

This is the smallest of the three species of *Myripristis* that are numerous on the nearshore Kona reefs. It remains secreted in small crevices

TABLE 15.—Food of *Holotrachys lima*.

Rank	Items	No. fish with this item (n = 10)	Mean percent of diet volume	Ranking index
1	Caridean shrimps	6	31.5	18.90
2	Xanthid crabs	5	33.0	16.50
3	Crab megalops	2	7.0	1.40
4	Fish	1	3.5	0.35
5	Gammaridean amphipods	1	0.5	0.05
Also, crustacean fragments		5	24.5	12.25

and coral interstices during the day, but emerges and aggregates in the lower levels of the water column, above the reef, about 30 min after sunset. After remaining active during the night, it returns to its daytime shelter on the reef about 30 min before sunrise (Hobson, 1972, as *M. multiradiatus*). When this fish is under cover during the day its body is solid red, but when active in the water column after dark, its lower sides are silvery, affording countershading like that described for nocturnally active *M. leiognathus* in the Gulf of California (Hobson, 1968a). This nocturnal pattern was illustrated earlier (Hobson, 1972: Figure 6).

Thirty-nine specimens (120: 74-145 mm) were speared at different times of the day and night. All 20 that were collected either over the reef at night (later than 4 h after sunset), or from shelter sites within an hour of sunrise, had their guts full of food. In contrast, 13 of 14 collected from shelter sites during the afternoon and evening twilight had empty guts (3 had a few fragments posteriorly in their intestines), and the 14th had in its stomach only well-digested fragments. Of the remaining five, collected above the reef early during the night (within 1 h after last light), four had their guts completely empty, indicating they had not as yet hunted successfully at that early hour, but the fifth was full of fresh calanoid copepods of a species that was exceptionally numerous around our diving lights for about 45 min shortly after last light on that particular evening. Items in the 22 individuals that contained identifiable material are listed in Table 16.

CONCLUSION.—*Myripristis kuntee* is a nocturnal planktivore that takes mostly crab megalops and other crustacea.

Myripristis murdjan (Forskål)

This holocentrid is numerous in Kona, where during the day it aggregates in reef crevices and under coral overhangs, especially where there is shelter from prevailing seas (Figure 14). The twilight activity of this species has been described (Hobson, 1972, as *M. berndti*). About 30 min after sunset it emerges from its daytime shelter and aggregates in the water column above the reef, generally rising to levels higher than those attained by *M. kuntee* (see above). Immediately, there is a general movement offshore. It remains uncertain how far it swims offshore —perhaps it does not go much beyond the drop-off into deep water, which is a major feeding ground for diurnal planktivores (Hobson, 1972). The offshore move is obscured by the circumstance that at any given time during the night many individuals of this species are swimming over the inshore reefs. Nevertheless, there are consistently fewer of them over inshore reefs on dark nights than on moonlit nights. Gosline (1965) also noted offshore migrations at night by species of *Myripristis* in Hawaii. About 40 min before sunrise this species begins to assemble above its diurnal shelter, and within 10 min all have taken cover for the coming day. This species shows essentially the same day-night difference in color patterns as *M. kuntee*, above.

Of 25 individuals (169: 139-270 mm) speared at different times of day and night, all 16 that were taken above the reef at night (later than 4 h after

TABLE 16.—Food of *Myripristis kuntee*.

Rank	Items	No. fish with this item (n = 22)	Mean percent of diet volume	Ranking index
1	Crab megalops	19	25.2	21.76
2	Decapod shrimps	9	11.8	4.83
3	Calanoid copepods	9	8.0	3.27
4	Mysids	7	9.3	2.96
5	Polychaetes	4	4.8	0.87
6	Fish	3	4.6	0.63
7	Stomatopods	4	2.8	0.51
8	Gammaridean amphipods	7	0.9	0.29
9	Gnathiid isopod larvae	2	1.8	0.16
10	Ostracods	2	0.1	0.01
11	Tanaids	1	0.1	0.01
12	Invertebrate eggs	1	0.1	0.01
Also,	crustacean fragments	14	27.8	17.69
	Unidentified fragments	3	2.7	0.37

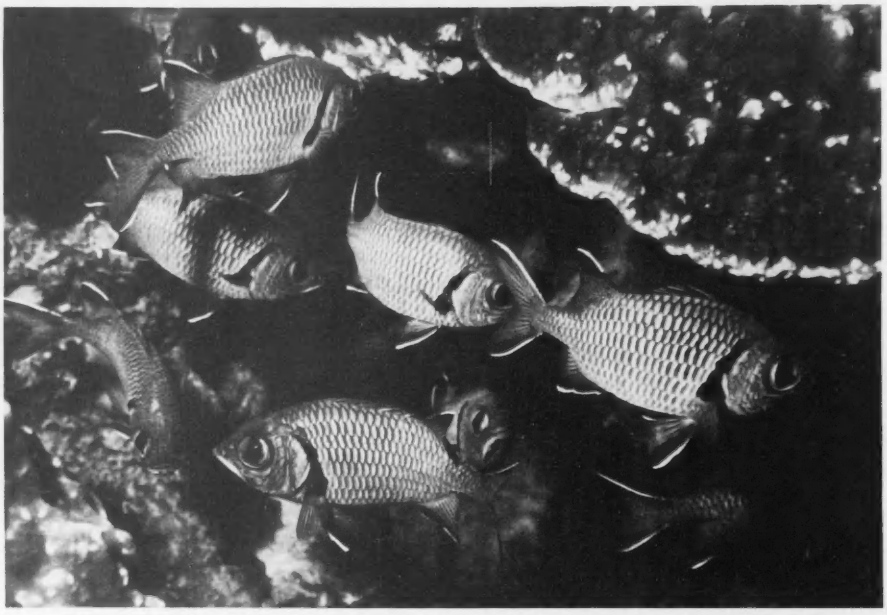

FIGURE 14.—*Myripristis murdjan*, a squirrelfish, aggregated under a coral ledge during the day.

sunset) contained food, whereas 8 of 9 that were collected from shelter sites during the afternoon were empty (the ninth specimen, collected during late afternoon, had only well-digested fragments in its stomach). Items in the 17 individuals containing identifiable material are listed in Table 17.

Hiatt and Strasburg (1960) found shrimp fragments in *M. murdjan* (reported as *M. berndti*) in the Marshall Islands, and suspected nocturnal habits, as did Randall (1955) for this species in the Gilbert Islands.

CONCLUSION.—*Myripristis murdjan* is a nocturnal planktivore that takes mostly crab megalops and other crustaceans.

Myripristis amaenus (Castelnau)

This squirrelfish, which congregates during the day in large caves cut into reefs exposed to an open-sea swell, is very similar to the preceding, *M. murdjan*, but is less numerous in most Kona habitats. Its behavior during twilight was described earlier (Hobson, 1972, as *M. argyromas*).

TABLE 17.—Food of *Myripristis murdjan*.

Rank	Items	No. fish with this item (n = 17)	Mean percent of diet volume	Ranking index
1	Crab megalops	16	53.5	50.35
2	Decapod shrimps	3	8.1	1.43
3	Mysids	3	6.5	1.15
4	Fish	2	2.0	0.24
5	Polychaetes	2	1.5	0.18
6	Stomatopods	2	0.9	0.11
7	Euphausiids	1	1.2	0.07
8	Cephalopods	1	1.2	0.07
9	Gammaridean amphipods	1	0.5	0.03
10	Prosobranch gastropods	1	0.3	0.02
11	Calanoid copepods	1	0.1	<0.01
12	Ostracods	1	0.1	<0.01
Also, crustacean fragments		8	14.5	6.82
	Unidentified fragments	4	9.6	2.26

Myripristis amaenus, like its congeners, emerges from its daytime retreats about 30 min after sunset, and at least many individuals move offshore, especially when there is no moonlight. *Myripristis amaenus* shows essentially the same day-night distinction in coloration that is described above for its congeners.

Of 19 individuals (176: 116-210 mm) speared at different times of day and night, all 14 collected above the reef at night (later than 4 h after sunset), or from shelter sites within 2 h after the species had returned to cover in the morning, contained food, whereas all 5 collected from shelter sites during late afternoon were empty. Items in the 14 individuals containing identifiable prey are listed in Table 18.

CONCLUSION.—*Myripristis amaenus* is a nocturnal planktivore that takes mostly crab megalops and other crustaceans.

General Remarks on Squirrelfishes

Squirrelfishes are known throughout tropical seas to hunt prey after dark. For example, they have been thus described in the Marshall Islands (Hiatt and Strasburg, 1960), the Gulf of California (Hobson, 1965, 1968a), and the West Indies (Randall, 1967). Similar behavior has been noted in the Florida Keys by Starck and Davis (1966), who noted there were no distinctive nocturnal color features in tropical Atlantic holocentrids, such as are reported for all but two of the Hawaiian species above.

The two major categories noted above in the introduction to the squirrelfishes each represents a generally different mode of predation. All feed primarily on crustaceans, but whereas species of *Holocentrus* and *Holotrachys lima* capture their prey close to the sea floor, species of *Myripristis* hunt prey up in the water column.

BOTTOM FEEDERS.—The seven holocentrids in this category feed mostly on benthic forms, but also take some prey that are free-swimming at the base of the water column. Xanthid crabs comprised the major prey item for all species except the largest, *Holocentrus spinifera,* which contained a slightly larger volume of caridean shrimps. Xanthid crabs are ubiquitous benthic animals in all Kona inshore habitats, and are widely active in exposed positions after dark.

Of the seven bottom-feeding squirrelfishes, only three similar species, *Holocentrus diadema, H. lacteoguttatum,* and *H. xantherythrus,* hunt significantly over sand in addition to feeding on hard reef substrata; however, even these three do not range away from cover during this activity, which is limited to sand pockets on the reef and only the fringes of more extensive sandy areas. Nevertheless, it is probably because of this habit that these three have more varied diets than do the others. Hiatt and Strasburg (1960) reported that some of the holocentrids in the Marshall Islands forage on sandy bottoms, citing sand-dwelling gastropods as being prominent prey of *H. diadema* in that area.

The other four bottom feeders, *Holocentrus sammara, H. spinifera, H. tiere,* and *Holotrachys lima,* restrict their activity largely to hard substrata on the reef, and prey more heavily on caridean shrimps—especially on snapping shrimps. Some of the larger individuals of *Holocentrus sammara* and *H. spinifera* capture the caridean *Saron marmoratus*; although individuals of this shrimp exceeding a length of 30 mm are numerous

TABLE 18.—Food of *Myripristis amaenus.*

Rank	Items	No. fish with this item (n = 14)	Mean percent of diet volume	Ranking index
1	Crab megalops	14	75.1	75.10
2	Decapod shrimps	4	9.3	2.66
3	Fish	3	2.9	0.62
4	Cephalopods	1	1.4	0.10
5	Mysids	4	0.3	0.09
6	Prosobranch gastropods	2	0.4	0.06
7	Polychaetes	1	0.4	0.03
8	Gammaridean amphipods	1	0.2	0.01
9	Calanoid copepods	1	0.1	<0.01
10	Stomatopods	1	0.1	<0.01
11	Isopods	1	0.1	<0.01
Also, crustacean fragments		8	9.7	5.54

in exposed positions on the reef after dark, most are too large to serve as prey for all but the biggest squirrelfishes.

WATER-COLUMN FEEDERS.—These are the species of *Myripristis,* all of which are primarily planktivores. This habit is reflected in their sharply upturned mouths, a feature well known as adaptive to feeding on plankton (e.g. Rosenblatt, 1967). Based on the food-habit data, crab megalops are the major prey of all three species reported here.

Earlier (Hobson, 1965, 1968a), I reported that *M. leiognathus* in the Gulf of California feeds in the water column after dark on planktonic crustaceans, including crab larvae. Similarly, Randall (1967) reported that *M. jacobus* in the tropical Atlantic feeds at night primarily on planktonic organisms, especially crustacean larvae, and Collette and Talbot (1972) noted that this species feeds at least 3 m above the reef. Probably similar habits are universal in species of *Myripristis.*

Order Gasterosteiformes

Family Aulostomidae: trumpetfishes

Aulostomus chinensis (Linnaeus)—*nunu*

This distinctive, solitary fish (Figure 15) is numerous on Kona reefs, where it attains the length of at least 700 mm. It exhibits three basic color forms: plain reddish brown, brown with light striping and other marks, and plain yellow. Several trumpetfish recognized as individuals were seen repeatedly in the same areas throughout the study, and none changed coloration during this time. The habitat of this species is in water deeper than about 5 m close to coral or irregular rocky substrata that offer many ledges and crevices.

I observed no difference in the behavior of this fish between day and night. At all hours it moves slowly, close to cover, propelling its long, cylindrical, rod-straight body mainly by undulating its soft dorsal and anal fins, which are set far back near the tail. The trumpetfish is a stalking predator, and on a few scattered occasions I saw it

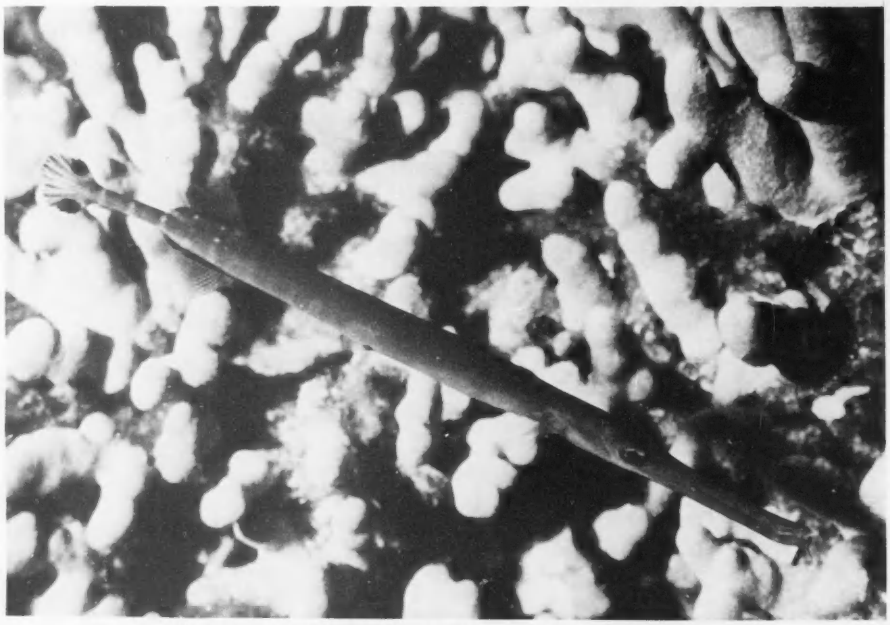

FIGURE 15.—*Aulostomus chinensis,* the trumpetfish, a stalking predator.

capture prey during daylight. After gaining a position close to its quarry, the attack is consummated with a short dart forward, the victim being literally sucked in with a sudden expansion of its tubular snout. Hiatt and Strasburg (1960) did not observe feeding, but speculated that this species in the Marshall Islands probes with its long snout in shallow holes and interstices of the reef and captures prey there by rapidly dilating its mouth. They found a small atherinid fish in the gut on one specimen. Sometimes trumpetfish accompany schools of grazing surgeonfishes—usually mixed groups of *Acanthurus sandvicensis* and *A. nigroris,* which frequently move across the reef. At these times, small organisms probably are driven out from algal cover by the grazing herbivores and become available as prey to the trumpetfish. Occasionally, the trumpetfish swims close beside large herbivores, especially parrotfishes, apparently using these large fishes as shields behind which to get close to prey not threatened by the herbivore.

Although 52 individuals (410: 220-621 mm) were speared at different times of day and night, no pattern was evident in the condition of the gut contents from specimens taken at these different times. Of 27 that contained food in their stomachs, 18 had captured fishes (mean percent of diet volume: 63; ranking index: 42), and 11 had taken caridean shrimps (mean percent of diet volume: 37; ranking index: 15.07).

It probably is significant that, with only two exceptions, those sampled had preyed on either fishes or shrimps—not both. The data cannot relate this selectivity to day or night activity or to size of predator. The 16 individuals that had preyed exclusively on fishes were within exactly the same size range (241-528 mm) as the 9 individuals that had preyed exclusively on shrimps. Furthermore, the mean sizes of the two groups differed only slightly—401 mm for the fish eaters, 396 mm for the shrimp eaters. The two individuals that had taken both fishes and shrimps were 241 and 337 mm long.

Aulostomus chinensis takes relatively large prey: the 15 fish items (representing among others *Apogon snyderi, Acanthurus nigrofuscus, Canthigaster* sp., and a labrid) that could be measured accurately had a mean standard length of 58 mm (range 25-88 mm) whereas the 11 shrimps that could be measured accurately had a mean total length of 55 mm (range 13-110 mm). Ten of the 11 shrimps were *Saron marmoratus,* the only shrimp this large that was numerous in exposed locations on the reef. Although this shrimp occupies exposed positions only at night, I have no evidence that it is taken by *Aulostomus chinensis* in greater numbers after dark.

Because the trumpetfish has an especially long, attenuated body, and because it takes relatively large prey, individuals that have recently ingested a meal often can be recognized by their distended bellies. Such individuals were occasionally seen during all periods of day and night, but most often during, or shortly after, twilight. Consistent with this, all three specimens that contained fresh prey (little or no damage by digestion) were collected during late twilight: in two of these instances (one in the morning, one in the evening) the prey were fishes; in the other instance (evening), the prey was a shrimp, *S. marmoratus.* Beyond this, the gut contents were of little help in establishing a pattern to feeding times; nor did the incidence of individuals with empty stomachs indicate a pattern, for they were collected during all periods of day and night.

CONCLUSION.—*Aulostomus chinensis* stalks prey, mostly fishes and caridean shrimps, most successfully during twilight, but also during the day and perhaps also at night.

General Remarks on Trumpetfishes

The activity of *Aulostomus chinensis* in Kona seems to be typical of the genus in other seas. Randall (1967) reported only fishes and caridean shrimps in 79 *A. maculatus* from the West Indies, and also remarked on the large size of these prey, as well as the way this trumpetfish sucks them into its mouth by expanding its tubular snout. Randall often observed *A. maculatus* hovering vertically in the water over small fishes and several times darting down on them (I did not see *A. chinensis* feed this way). Collette and Talbot (1972) judged *A. maculatus* in the Virgin Islands to be primarily crepuscular. They were uncertain about its nocturnal activity, but judged one they saw in a gorgonian at 2330 h to be quiescent. Eibl-Eibesfeldt (1955) described the way trumpetfish in the Indian Ocean use other fishes as cover behind which to approach small prey, and this was also reported by Collette and Talbot (1972) from the Virgin Islands.

Family Fistulariidae: cornetfishes

Fistularia petimba Lacépède

The cornetfish (see Hobson, 1968a: Figure 9) looks much like the trumpetfish, but grows considerably larger, many being over 1 m long. It is a pale-green fish with light-blue markings, and under certain circumstances instantaneously displays a series of broad bands along its body. Earlier I (Hobson, 1968a) reported that this species in the Gulf of California displays these bands when poised to strike prey. In Kona, the bands appear in similar circumstances and also in situations that suggest the fish might feel threatened, as when it is approached underwater by a human—especially a human carrying a diving light at night. *Fistularia petimba* frequently swims in loosely spaced groups of several individuals, generally in exposed shallowwater locations over the reef top.

Occasionally, *F. petimba* was seen in Kona stalking its prey during daylight, as observed in the Gulf of California (Hobson, 1968a). It does not move suddenly until within a few centimeters of its prey. When positioned for attack, it often draws its midsection into a modified "s" (as viewed from above), then darts forward for the capture. *Fistularia petimba* is more agile than *A. chinensis,* and undulating body movements not seen in the latter are regularly used to provide greater thrust in attacks and accelerated swimming. In the Gulf of California, I saw *F. petimba* use other fish as shields behind which to approach prey, as described above for *A. chinensis,* but did not see this in Kona. The behavior of *F. petima* was not seen to differ between day and night.

The 10 specimens (673: 363-1,069 mm), although collected during both day and night, were too few to provide much evidence on feeding times; however, of the 2 with empty guts, 1 was collected during late afternoon, and the other just before first morning light, indicating that these 2 had not fed during the preceding day and night, respectively. Only two specimens contained fresh prey, and both were collected shortly after twilight —one after evening twilight, the other after morning twilight. Though limited, these data suggest crepuscular feeding. Although prey in the other six specimens were in stages of digestion not inconsistent with predominantly crepuscular feeding, they clearly showed that prey are also taken at other times. All eight individuals with material in their stomachs had fed on fishes exclusively; only two prey could be identified to species, one a 70-mm cardinalfish, *Apogon snyderi,* the other a 52-mm damselfish, *Abudefduf imparipennis.* Both of these prey could have been captured close to reef crevices during the day.

Thus, *F. petimba* in Kona, as in the Gulf of California (Hobson, 1968a), was found to prey only on fishes. Hiatt and Strasburg (1960) also reported this species in the Marshall Islands to be exclusively piscivorous. My data suggest that *F. petimba* takes somewhat smaller prey than does *A. chinensis* of comparable length, as might be expected in view of the deeper body and snout of the latter. The mean length of the seven *F. petimba* containing measurable prey was 593 mm (range: 363-795 mm). The 11 measurable prey in these individuals had a mean length of 32 mm (range: 8-70). Comparable data for *A. chinensis* are given above.

CONCLUSION.—*Fistularia petimba* stalks fishes most successfully during twilight, but also during the day and perhaps at night.

General Remarks on Cornetfishes

The exclusively piscivorous habits of *Fistularia petimba* are paralleled by the similar diet of *F. tabacaria* in the tropical Atlantic (Randall, 1967). Suyehiro (1942) claimed that *F. petimba* feeds on tiny floating organisms by using its snout like a pipette, but I join Hiatt and Strasburg (1960) and Randall (1967) in contesting this opinion of the size of its prey. Starck and Davis (1966) found *F. tabacaria* to be more numerous on Florida reefs at night than during the day, but did not speculate that this reflected differences in feeding behavior.

Order Scorpaeniformes

Family Scorpaenidae: scorpionfishes

Pterois sphex Jordan and Evermann — lionfish, *nohu pinao*

The lionfish is a sluggish, solitary species that usually rests motionless on the reef, yet draws attention by its spectacular appearance (Figure 16). Perhaps because its fin spines carry a potent toxin, this fish makes little effort to evade a human collector. It is not numerous in Kona, and

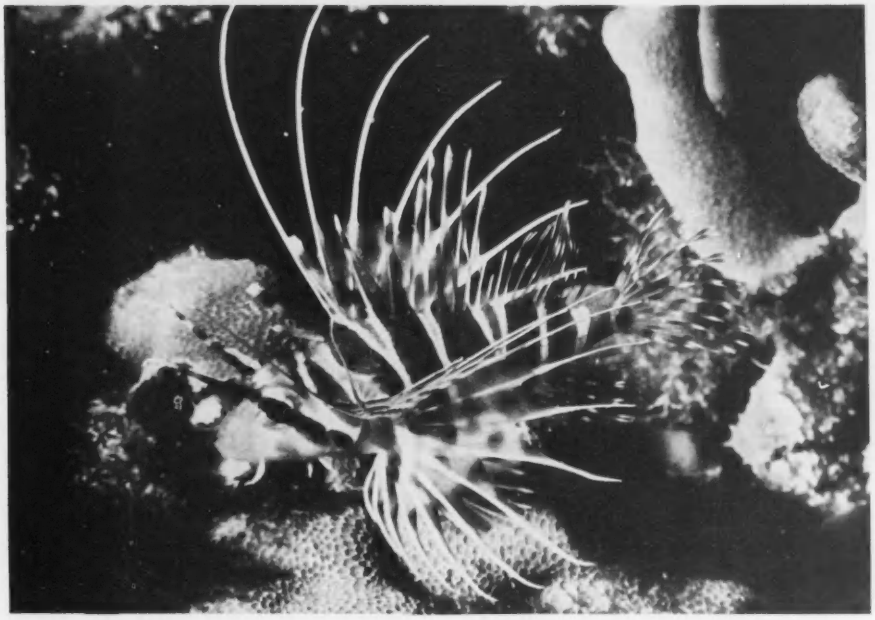

FIGURE 16.—*Pterois sphex*, a lionfish, swimming close to the reef at night.

occurs in visible locations on the reef most often after dark—though never far from shelter.

Fourteen specimens (83: 58-121 mm) were speared during day and night. Of nine that were collected during the afternoon or evening twilight, the guts in six were empty, and three had only well-digested crustacean fragments in their stomachs. On the other hand, all five specimens collected at night (more than 2 h after sunset) contained relatively fresh prey in their stomachs.

All eight specimens that contained food had fed on crustaceans exclusively. Caridean shrimps, which occurred in six, were the major food item (mean percent of diet volume: 56.3; ranking index: 42.19). Other food items were: xanthid crabs in three (mean percent of diet volume: 13.8; ranking index: 5.16) and pagurid crabs in one (mean percent of diet volume: 0.6; ranking index: 0.08). Five individuals contained unidentified crustacean fragments (mean percent of diet volume: 29.4; ranking index: 18.36).

CONCLUSION.—*Pterois sphex* is a nocturnal predator that takes benthic crustaceans, especially caridean shrimps.

Scorpaena coniorta (Jenkins)

Although this small species is the most numerous scorpaenid on Kona reefs, the casual observer will encounter it only at night. During the day individuals more than about 50 mm long are deep in reef crevices, whereas many smaller individuals are motionless among the branches of the coral *Pocillopora meandrina* (Figure 17). After nightfall, many of these fish occur in exposed positions: the larger individuals are spread widely across the reef, resting immobile on rock or coral, whereas the smaller ones are perched motionless on the sea floor close by the same coral heads that shelter them during the day. However, at any given time of night some of these fish are among the coral branches, just as in daylight.

Thirty-four specimens (46: 36-67 mm) were collected during various times of day and night. Of 12 that were taken during afternoon or early evening, most from among coral branches, only 1 had food in its gut (3 had a few fragments posteriorly in their intestine). The one containing food, taken from a coral head, had in its stomach a crab that, based on damage by digestion, probably had been

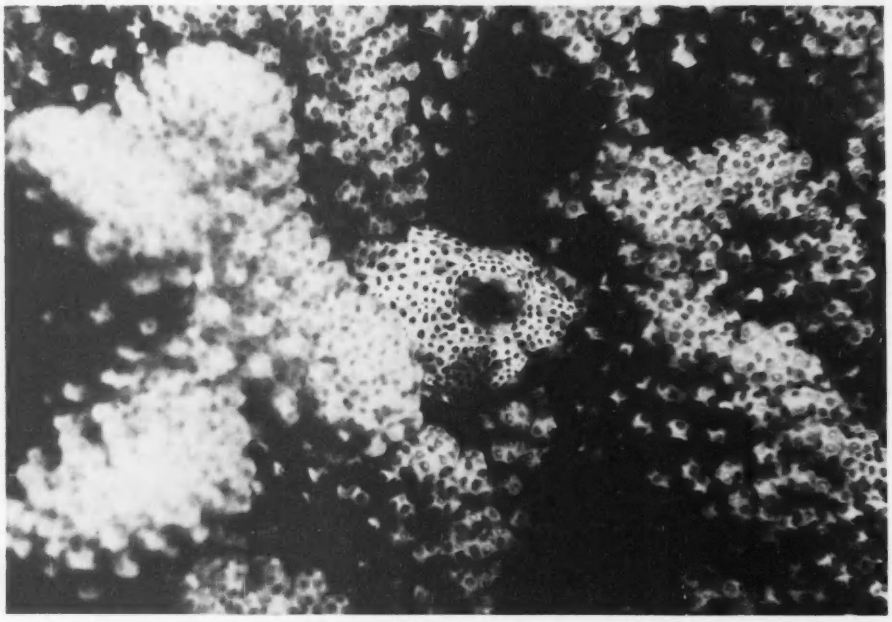

FIGURE 17.—*Scorpaena coniorta*, a scorpionfish, nestled among coral branches during the day.

captured during the day. In comparison, 14 of 22 individuals collected at night, between 3 h after sunset and first morning light, had food in their stomachs. Brachyuran crabs, almost all of them xanthids, occurred in 7 of the 15 individuals that contained identifiable items (mean percent of diet volume: 39; ranking index: 18.2). Caridean shrimps occurred in six (mean percent of diet volume: 28.3; ranking index: 11.33), and fishes in one (mean percent of diet volume: 6.7; ranking index: 0.45). Unidentified crustacean fragments occurred in six (mean percent of diet volume: 26; ranking index: 10.4). Many of the xanthids and carideans found in specimens less than 50 mm long are forms that cooccur with these fish among the coral branches.

CONCLUSION.—*Scorpaena coniorta* is a nocturnal predator that takes benthic crustaceans, mostly xanthid crabs and caridean shrimps. Some prey are also captured during the day.

Scorpaenopsis cacopsis* Jenkins—*nohu 'omakaha

This species, the largest Hawaiian scorpaenid, grows to over 50 cm long (Gosline and Brock, 1960). I observed no overt difference in its behavior between day and night as it was seen resting immobile on the reef at all hours, often fully exposed. Despite its large size and frequent disdain for cover, this fish remains virtually unseen, owing to body hues and texture that render it much like the reef on which it rests. It was not seen feeding, but its morphology and behavior suggest that it lunges forward to attack prey that have strayed within range, and sucks them in with a sudden expansion of its cavernous mouth.

Of the five specimens (256: 73-375 mm) examined, three had prey in their stomachs: one, taken within 1 h after sunrise, contained a fresh fish, *Pomacentrus jenkinsi* (104 mm); a second taken at night, 4 h after sunset, contained a relatively fresh octopus; and the third, taken late in the afternoon, contained fish fragments. The other two, both empty, were collected during morning twilight.

CONCLUSION.—*Scorpaenopsis cacopsis* attacks fishes and motile invertebrates during the day. Its nocturnal activity remains uncertain.

General Remarks on Scorpionfishes

Scorpionfishes on tropical reefs are widely described as predators that rest on the bottom, and

because they resemble their surroundings they remain unseen by small prey that swim within striking range (Longley and Hildebrand, 1941; Hiatt and Strasburg, 1960; Starck and Davis, 1966; Randall, 1967). This behavior is descriptive of some scorpaenids, but probably is overdrawn as a generalization encompassing the entire family. Such a tactic is adaptive to daylight, and is used by *Scorpaenopsis cacopsis* in Hawaii (the one fish identified as prey of this predator, a damselfish, is strictly a diurnal species that is not active over the reef at night). Significantly, the fishes that have been reported by other investigators as prey of scorpaenids on tropical reefs similarly imply diurnal predations: blennies (Longley and Hildebrand, 1941); a wrasse and a parrotfish (Hiatt and Strasburg, 1960); and an angelfish, a surgeonfish, a sardine, a sea horse, and a conger eel (Randall, 1967). With perhaps the lone exception of the conger eel, these are fishes that swim close to the reef during daylight, and at that time would be vulnerable to the ambushing tactic of scorpaenids; however, they would not be readily available after dark when most of them rest under cover on the reef or, in the case of the sardine, swim away from the reef. Conspicuously absent among the reported prey are the many species of comparable size that are numerous close above the reef at night, including apogonids and holocentrids. One can readily see how camouflage and ambush would be especially suited to daylight, but less significant after dark. Randall (1967), basing his generalization on the West Indian situation, characterized the scorpaenids as diurnal. In Hawaii, most species are predominantly nocturnal. In addition to *Pterois sphex* and *Scorpaena coniorta*, which prey largely on benthic crustaceans, as described above, other members of the family that appear on the reef in greater numbers at night include *Dendrochirus brachypterus*, *Scorpaenodes parvipinnis*, and *Scorpaena ballieui*. Among feeding scorpaenids, camouflage does not seem to play the important role at night that it does during the day. When these predators are abroad after dark they often contrast markedly with their surroundings. Although fishes do not seem to be significant prey at night, the behavior of these nocturnal scorpaenids indicates that their tactic remains a short lunge from a resting position to capture prey that have inadvertently come within range.

Order Perciformes

Family Serranidae: sea basses

Sea basses are prominent on most tropical reefs, but the family has no representatives native to shallow Hawaiian reefs (Gosline and Brock, 1960). Nevertheless, the widespread Indo-Pacific serranid *Cephalopholis argus* has been introduced into Hawaii from the Society Islands, the first time in 1956, and has since become well established in Kona.

Cephalopholis argus Bloch and Schneider

This solitary fish, numerous on Kona reefs, swims close among overhanging ledges and crevices during the day, but is seen less often at night. Because it generally is wary of humans, lack of nocturnal observations could mean that it avoided our diving lights at night.

Although 6 of 10 specimens (319: 232-520 mm) speared at various times of day were empty, no temporal pattern is recognized, as the 6 were taken from early morning to late afternoon. All four that contained food, also taken at various times during the day (on four different occasions over 3 mo), had fed exclusively on fishes. One, taken during midmorning, contained, because of digestion, what was recognizable only as a fish (125 mm). The other three—one collected during midday, and two late in the afternoon—each contained a single moderately digested squirrelfish, *Holocentrus xantherythrus* (80, 110, and 130 mm, respectively). *Holocentrus xantherythrus* congregates under ledges during the day in areas where *C. argus* is active (see the species account for *H. xantherythrus* above), and thus is available as prey for the sea bass at this time. *Cephalopholis argus* has been reported to feed on shrimps as well as fishes in the Marshall Islands (Hiatt and Strasburg, 1960) and on shrimps in the Gilbert Islands (Randall, 1955). In a sample of 98 specimens from Tahiti, Randall and Brock (1960) found that 77.5% contained fishes, whereas 22.5% contained crustaceans (shrimps and crabs).

CONCLUSION.—*Cephalopholis argus* preys on fishes among reef crevices during the day. Its nocturnal habits remain uncertain.

General Remarks on Sea Basses

Diurnal piscivorous habits were reported in *Mycteroperca rosacea* in the Gulf of California,

with peaks during twilight (Hobson, 1965, 1968a). On the other hand, nocturnal habits were noted in *Alphestes multiguttatus* and *Rypticus bicolor* (the latter is often placed in a separate family, the Grammistidae), both of which prey chiefly on benthic crustaceans (Hobson, 1965, 1968a). In the same reports, a fourth sea bass, *Epinephelus labriformis,* was reported to feed by both day and night, chiefly on fishes in daylight and on benthic crustaceans after dark. These data suggest that fishes may be the major prey of sea basses in daylight with crustaceans predominating after dark, a generalization consistent with the limited observations on *Cephalopholis argus* in Kona.

Starck and Davis (1966) noted that serranids of the genera *Epinephelus, Mycteroperca,* and *Petrometopon* behave similarly day and night in the Florida Keys, with probable feeding peaks around sunrise and sunset. Longley and Hildebrand (1941) reported that *Epinephelus morio* feeds during both day and night in the Dry Tortugas, Fla., and Randall (1967) noted that larger serranids in the West Indies feed both day and night, with greatest activity at dawn and dusk. Collette and Talbot (1972), on the other hand, reported *E. guttatus* in the Virgin Islands to be active by day and apparently asleep at night. They also found *E. fulvus* and *E. cruentatus* active in daylight and suspected that these sea basses rest at night. Randall (1967) considered the smaller serranids, in general, to be primarily diurnal. In Florida, Starck and Davis (1966) regarded certain small serranids of such genera as *Diplectrum, Hypoplectrus,* and *Serranus* to be active by day and inactive by night. None of these authors attempted to relate time of activity with kinds of prey.

Family Kuhliidae: aholeholes

Kuhlia sandvicensis* (Steindachner)—*aholehole

This predator occurs in only a few locations within the Kona study area, and there just sparsely, compared to its large numbers elsewhere in Hawaiian nearshore waters. Juveniles and young adults live in tide pools or in schools close to shore (Gosline and Brock, 1960), but the larger adults congregate during the day under low ledges and boulders, usually in water less than 5 m deep farther from shore. They emerge from shelter at nightfall, and the few observed after dark during this study were solitary in the water column over the reef. Gosline and Brock (1960) noted that the adults, at least, are nocturnal, a conclusion consistent with the large eyes of the species.

Of the 13 specimens (164: 132-202 mm) collected, 8 speared during midmorning from under rocky cover contained in their stomachs extensively digested crustacean fragments (including crab megalops), 1 taken under a rock at noon contained only well-digested material scattered through its intestine, and 4 speared under rocks late in the afternoon were empty.

CONCLUSION.—*Kuhlia sandvicensis* is a nocturnal predator that feeds on free-swimming crustaceans.

Family Priacanthidae: bigeyes

Priacanthus cruentatus* (Lacépède)—bigeye, *aweoweo

This priacanthid (Figure 18) is numerous in Kona, where it takes shelter under rocks or coral during the day, often in groups, and is active in the open at night. After emerging from shelter at nightfall, many individuals assemble in schools high in the water column and then migrate offshore. These do not return inshore until about 40 min before sunrise, but a lesser number of other individuals, mostly solitary or in small groups, remain over the inshore reefs throughout the night. All of these fish return to their daytime shelter by 30 min before sunrise, at least many of them to specific home caves (Hobson, 1972).

Forty specimens (173: 115-255 mm) were collected during day and night. All 17 that were speared during morning twilight (shortly after they had reappeared near their diurnal shelter, but before they had taken cover) had relatively fresh prey in their stomachs. Four others were collected from under cover during late morning, and although all had full stomachs, with many items identifiable, digestion was advanced, and most of the material was damaged beyond recognition. The other 19 were collected from caves late in the afternoon, and although only 4 of these had empty stomachs, the material in the other 15 was reduced to unidentified fragments. Items in the 21 specimens containing identifiable material are listed in Table 19.

Hiatt and Strasburg (1960) acknowledged that species of *Priacanthus* generally are thought to be nocturnal, but contested this opinion as far as *P.*

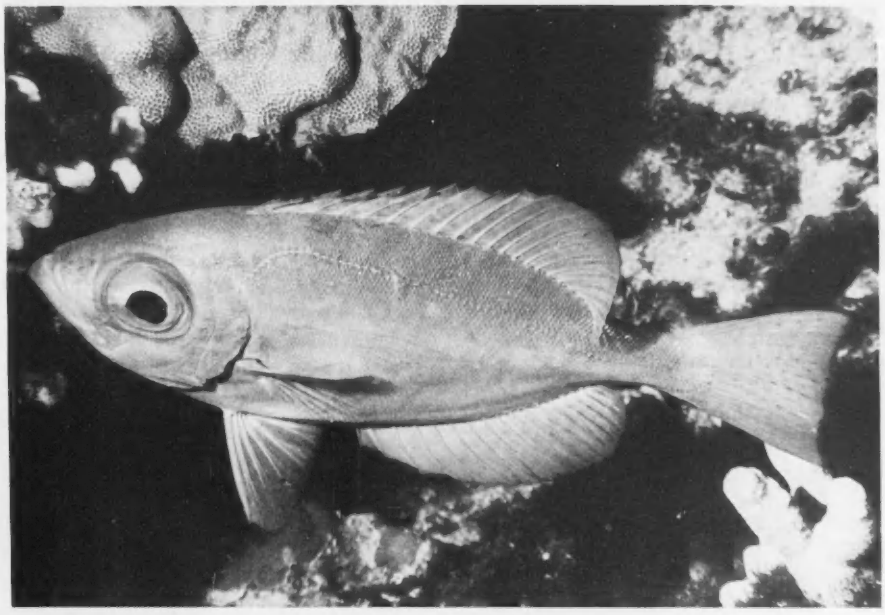

FIGURE 18.—*Priacanthus cruentatus*, a bigeye, showing the plain red coloration typical of this species when among the coral during the day.

cruentatus in the Marshall Islands is concerned. Although conceding the possibility of some nocturnal feeding, they believed that this species captures octopods, a major food there, in reef crevices and caves during the day. This conclusion was heavily influenced by finding food in the stomachs of this priacanthid during the day, but none in stomachs of the nocturnally active holocentrids. As noted above, I found a similar difference between *P. cruentatus* and holocentrids in Kona, but attribute this to the priacanthid retaining food in its stomach longer during digestion than do holocentrids.

Longley and Hildebrand (1941) noted that this circumtropical species feeds chiefly at night in Florida, a conclusion with which Starck and Davis (1966) concurred. In the West Indies, Randall (1967) was of the same opinion, but he also felt that the condition of prey in some specimens indicated diurnal feeding as well; Randall noted that *P. cruentatus* preys mostly on the larger animals in the plankton. Collette and Talbot (1972) concluded that in the Virgin Islands this is a crepuscular species that continues to feed in caves and under ledges during daytime.

Gosline (1965) reported that *P. cruentatus* in

TABLE 19.—Food of *Priacanthus cruentatus*.

Rank	Items	No. fish with this item (n = 21)	Mean percent of diet volume	Ranking index
1	Crab megalops	17	32.3	23.15
2	Cephalopods	8	20.4	7.77
3	Fish	6	11.2	3.20
4	Decapod shrimps	5	3.6	0.86
5	Adult crabs	2	7.6	0.72
6	Mysids	1	0.4	0.02
7	Stŏmatopods	1	0.1	0.01
Also, crustacean fragments		11	13.4	7.02
	Unidentified fragments	8	11.0	4.19

Hawaii migrates offshore at night. In Florida, however, Starck and Davis (1966) noted only that it is active at night in the same areas where it is sheltered in daylight; they illustrated this species with a mottled color pattern, which they believed to be its nocturnal coloration. The same mottled pattern occurs regularly at night in Kona when the fish is held in the beam of a diving light, and I believe it is a response to the light, rather than a nocturnal coloration—especially because the pattern is intensified upon moving the light progressively closer to the fish. In the absence of a diving light at night, this species is either plain red (as it usually is in daylight), or, more often with individuals in mid-water, overall pale-silver (occasionally this pale-silver coloration is displayed under cover during the day). The blotched pattern is the red and silver hues in combination.

CONCLUSION.—*Priacanthus cruentatus* is a nocturnal predator that feeds on free-swimming organisms, mostly crustaceans and cephalopods.

Family Apogonidae: cardinalfishes

Apogon erythrinus Snyder

After dark, this small solitary cardinalfish is numerous close to basalt reefs in water less than 6 m deep, usually in small sand and cobble pockets. The smaller ones are largely transparent, and transparency remains a characteristic of even the largest individuals, despite an increased pinkish hue (Figure 19). During the day *A. erythrinus* remains out of sight, secreted deep in reef crevices.

Of 14 individuals (36: 22-42 mm) examined, 4 that had been collected together from a deep crevice 4 h after sunrise were empty (rotenone was used to collect these 4, a departure from the standard collecting method necessary here because the species was never visible during the day). The other 10 specimens were speared from among those active in exposed locations on the reef at night (more than 4 h after sunset), and although 2 were empty, the other 8 contained prey in their stomachs.

All eight with material in their stomachs contained crustaceans exclusively. Xanthid crabs

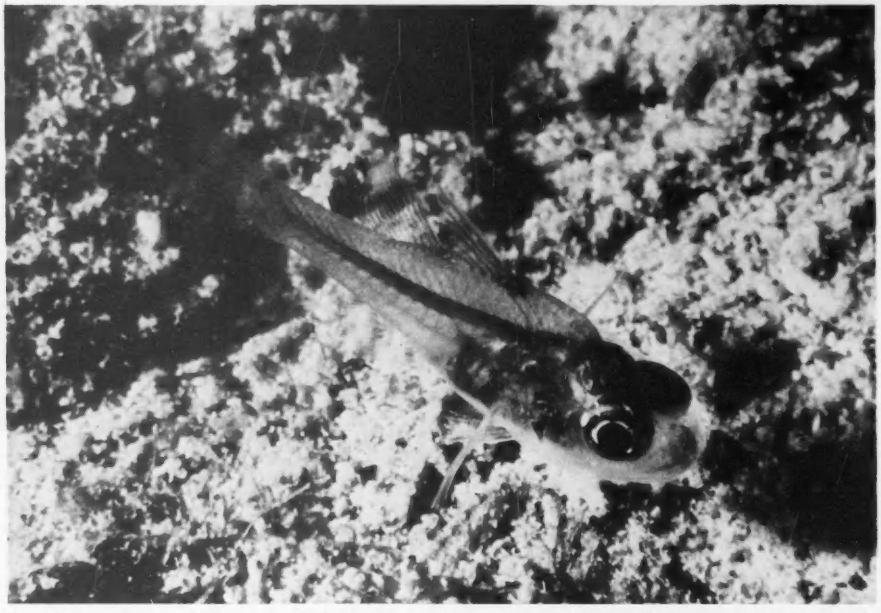

FIGURE 19.—*Apogon erythrinus*, a cardinalfish, showing the transparency typical of this species as it swims close to the reef at night.

were the major item, occurring in five individuals (mean percent of diet volume: 50; ranking index: 31.25). Most of these xanthids were in the megalops stage, except that their abdomens were reflected under their carapaces. The only other identifiable prey, occurring in three specimens, were gammaridean amphipods (mean percent of diet volume: 20; ranking index: 7.5). Four contained unidentified crustacean fragments (mean percent of diet volume: 30; ranking index: 15).

CONCLUSION.—*Apogon erythrinus* is a nocturnal predator that takes mostly benthic crustaceans.

Apogon menesemus Jenkins—*'upapalu*

This species and the very similar *A. snyderi* (below) are the largest and most abundant apogonids in Hawaii (Gosline and Brock, 1960), and they were the apogonids seen most often during the present study. During the day, *A. menesemus* hovers quietly in the deep shadows of reef crevices, but during late evening twilight emerges into the open. Throughout the night solitary individuals hover about 1 m above the coral. On several occasions after dark this cardinalfish struck at the silver barb on my otherwise dark spear: sometimes when this happened the spear was faintly illuminated by my partner's diving light, but other times moonlight provided the only illumination. At first morning light *A. menesemus* moves close to cover on the reef, and during morning twilight returns to its daytime shelter. When under cover during the day its coloration is relatively featureless, but when in the open at night distinctive fin markings appear (Figure 20a and b).

Fifty-nine specimens (114: 90-134 mm) were collected during day and night. Of the 14 that were speared from reef caves during late afternoon, only 2 had food in their stomachs—one contained an extensively digested piece of meat that probably was the remains of prey captured the previous night, whereas the other contained a relatively fresh xanthid crab that appeared to have been captured earlier that day. In comparison, 25 of 40 specimens collected at night, between 3 h after sunset and first morning light, had food in their stomachs—much of it fresh. Finally, of five specimens collected from caves during early morning, within 3 h after sunrise, four had food in their stomachs. Items in the 31 individuals containing identifiable material are listed in Table 20.

Two individuals that each contained just a single xanthid crab are the only ones that indicated exclusively benthic feeding; significantly, one of these was the lone individual, noted above, that appeared to have fed while under cover during the day. The other, collected in the open just 3 h after sunset, may also have taken its prey before leaving shelter in the evening. *A. menesemus* takes mostly free-swimming prey, presumably at its regular nocturnal station above the reef. Nevertheless, judging from the sand mixed with food in one individual collected at midnight, some prey are taken from the sea floor after dark.

CONCLUSION.—*Apogon menesemus* is a nocturnal predator that feeds mostly on free-swimming crustaceans.

Apogon snyderi Jordan and Evermann—*'upapalu*

This cardinalfish cooccurs with the very similar *A. menesemus*, above, but the two species remain at least partially segregated. During the day both species occupy the same caves, but *A. snyderi* is not so deep in the shadows and, in fact, frequently hovers at the entrances. Like *A. menesemus*, *A. snyderi* emerges into the open during evening twilight, but during the night stays closer to the sea floor; furthermore, whereas *A. menesemus* mostly remains over coral, *A. snyderi* tends to move over the sand patches within the reef and in the fringes of the more extensive sand areas adjacent to the reef. On several occasions at night, *A. snyderi* struck at the silver barb on my spear, just as described above for *A. menesemus*. *Apogon snyderi* does not have prominent nocturnal color features, as does *A. menesemus*. When over sand at night its body has a highly reflective bluish cast, also shown to a lesser extent by *A. menesemus*, but which is largely lost by both species soon after they move over coral or rocks.

Thirty specimens (96: 82-130 mm) were speared during day and night. All 3 that were taken from caves during the afternoon had empty stomachs, whereas of 24 collected in the open at night, between 2 h after sunset and first morning light, 22 had food in their stomachs. The remaining three were collected from caves during the 4 h after sunrise, and while two of these had food in their stomachs, the third was empty. Items in the 24 individuals containing identifiable material are listed in Table 21.

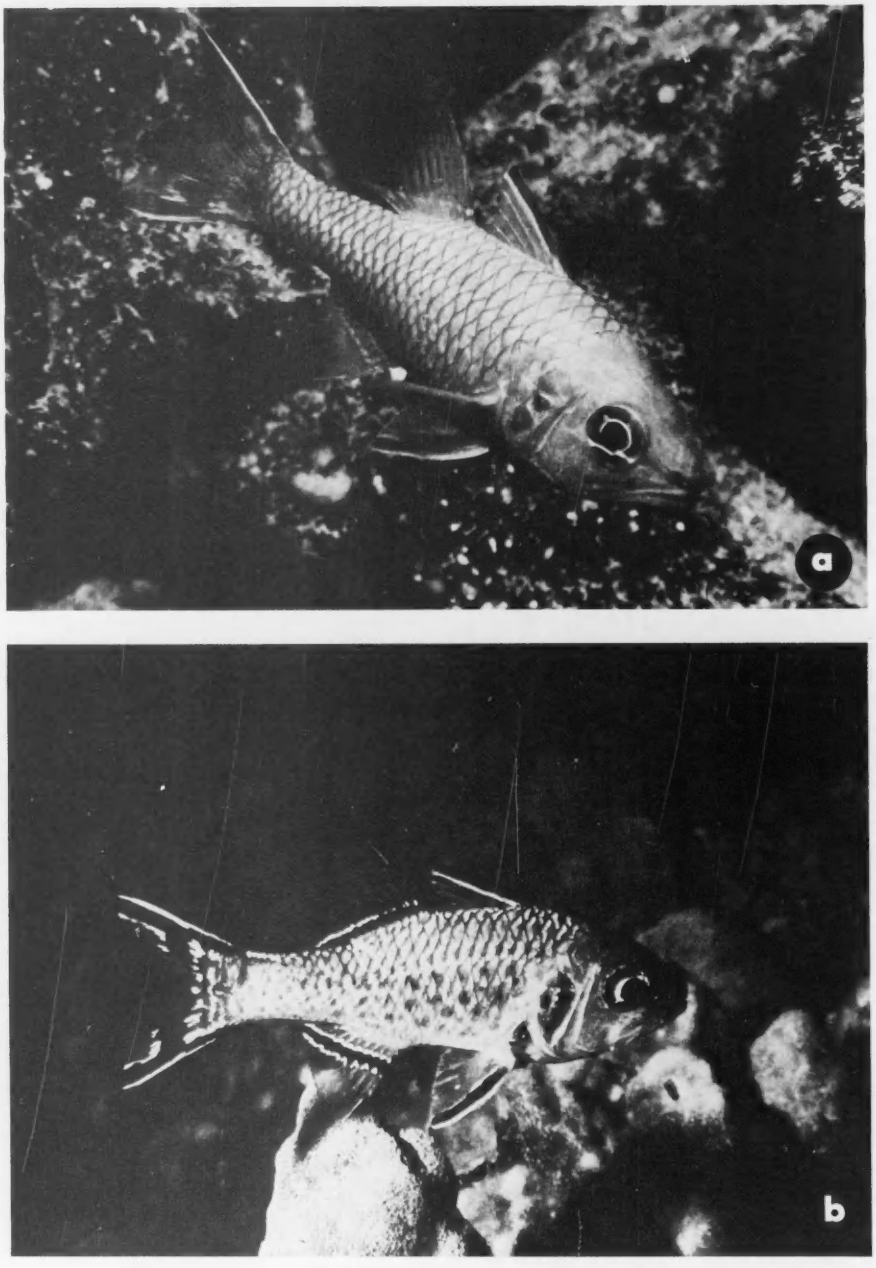

FIGURE 20.—*Apogon menesemus*, a cardinalfish: a, showing its diurnal coloration under a ledge during the day; b, showing its nocturnal coloration as it swims above the reef at night.

TABLE 20.—Food of *Apogon menesemus*.

Rank	Items	No. fish with this item (n = 31)	Mean percent of diet volume	Ranking index
1	Crab megalops	10	17.6	5.68
2	Decapod shrimps	11	15.7	5.57
3	Xanthid crabs	2	6.9	0.45
4	Mysids	3	2.9	0.28
5	Fish	1	2.0	0.07
6	Gammaridean amphipods	1	0.8	0.03
7	Isopods	1	0.2	<0.01
8	Copepods	2	0.1	<0.01
9	Gastropod larvae, echinospira	1	0.1	<0.01
Also, crustacean fragments		20	40.0	25.81
	Unidentified fragments	6	13.7	2.65

TABLE 21.—Food of *Apogon snyderi*.

Rank	Items	No. fish with this item (n = 24)	Mean percent of diet volume	Ranking index
1	Decapod shrimps	12	34.3	17.15
2	Xanthid crabs	6	14.6	3.65
3	Crab megalops	4	7.5	1.25
4	Fish	2	5.6	0.47
5	Mysids	2	2.1	0.18
6	Hippid crabs	1	4.2	0.18
7	Polychaetes	1	2.9	0.12
8	Copepods	1	1.3	0.05
9	Gammaridean amphipods	1	1.3	0.05
10	Sipunculid introverts	1	0.2	<0.01
Also, crustacean fragments		12	25.4	12.70
	Unidentified fragments	1	0.6	0.03

The diet of *A. snyderi*, compared with that of *A. menesemus*, includes a greater proportion of benthic organisms, especially forms from sandy bottom, like hippid crabs. Nevertheless, many of the prey of *A. snyderi* are free-swimming forms that may or may not have been in the water column when captured. The major item, decapod shrimps, were mostly in their planktonic larval stage.

CONCLUSION.—*Apogon snyderi* is a nocturnal predator that feeds on both free-swimming and benthic forms, mostly crustaceans.

General Remarks on Cardinalfishes

Cardinalfishes are widely recognized as being nocturnal. For example, Starck and Davis (1966) reported that all of the apogonids they studied in Florida Keys are nocturnal, and Randall (1967) came to the same conclusion for species in the West Indies; Randall provided food-habit data on two forms, *Apogon conklini* and *A. maculatus*, both of which prey primarily on plankton.

In the Gulf of California, *A. retrosella*, a relatively small nocturnal species (mostly <100 mm long), aggregates above the reef at night, preys on plankton, and its aggregations are more compact under moonlight than on dark nights (Hobson, 1965, 1968a). Although the relatively large *A. menesemus* is solitary when feeding on free-swimming prey above Kona reefs, it remains within about 1 m of the reef, never far from cover.

Another apogonid occasionally seen in Kona, *A. maculiferus*, has behavior more like that of *A. retrosella* in the Gulf of California. *Apogon maculiferus* is abundant on some Hawaiian reefs and attains a length of about 150 mm (Gosline and Brock, 1960). It was not abundant during this study, however, and all those seen apparently were juveniles that ranged between about 20 and 60 mm long. On nights of bright moonlight these small individuals were in aggregations 2 to 3 m above the reef; however, on dark nights they ranged even higher in the water column, their aggregations were more loosely formed, and many of them were solitary. Significantly, limited observations indicate that juveniles of both *A. menesemus* and *A. snyderi* (< 50 mm long) behave

more like these small individuals of *A. maculiferus* than they do like the adults of their own species, so this behavior may be characteristic only of the smaller representatives of all three species.

Finally, a fourth apogonid, *Pseudamiops gracilicauda*, is relatively numerous in Kona, but does not seem to grow longer than about 30 mm. Being such a small species, *P. gracilicauda* generally went unnoticed by me and, in fact, was seen only on dark nights when solitary individuals hovered 1 to 2 m above the reef.

Suyehiro (1942), Hiatt and Strasburg (1960), and Hobson (1965), all reported that certain apogonids cease to feed sometime during reproductive activity. Perhaps this phenomenon accounts for the relatively high incidence of empty stomachs at night in *A. menesemus* from Kona (15 of 40), especially considering that species of other nocturnal groups with similar diets, like the various holocentrids (see above), are almost always full of food at night.

E. H. Chave, University of Hawaii, is currently working on the ecology of Hawaiian apogonids.

Family Carangidae: jacks

The jacks are prominent fishes on Hawaiian reefs, but although many species were seen occasionally during this study, only one, presented below, was observed regularly.

Caranx melampygus Cuvier—blue ulua, *'omilu*

This jack (Figure 21), attains a length of about 1 m in Hawaii (Gosline and Brock, 1960), but most of those present in Kona during this study were less than half this size. During the day it usually is solitary, or in groups of several individuals. Typically, it swims actively about 1 m above the reef in a manner that suggests it is patrolling over a relatively large area. Frequently several of these jacks accompany the large piscivorous goatfish, *Parupeneus chryserydros* (see account for this species, below), probably to capture prey that are driven out of hiding as the goatfish probes the substratum. This jack swims over the reef throughout the day, but occurs there most frequently during early morning and late afternoon

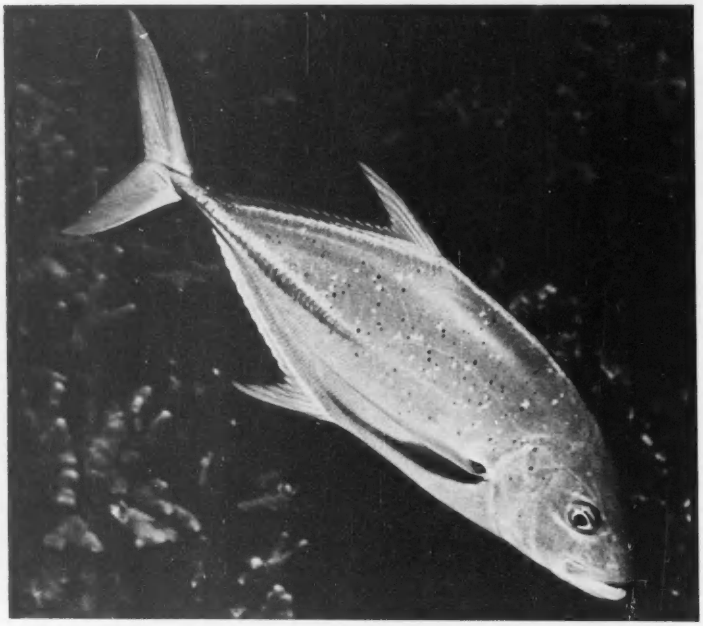

FIGURE 21.—*Caranx melampygus*, a jack, swimming close above the reef during the day.

or evening. It was only occasionally seen at night, perhaps because it avoided our diving lights after dark.

Six specimens (337: 245-570 mm) were collected at various times of the day. The only one (248 mm) that contained relatively fresh prey (three larval fishes, about 10 mm long, and a number of mysids) was collected 3 h after sunrise. A second individual (315 mm), taken shortly after noon, contained in its stomach, an unidentified fish (about 80 mm) and a shrimp, both moderately digested. Three other individuals (245-330 mm) were collected late in the afternoon, and their stomachs contained well-digested fragments—in at least one, the fragments of a fish. The last specimen (570 mm) behaved as if sick when speared early in the afternoon, and its gut was empty. Hiatt and Strasburg (1960) found only fishes in the two specimens of this species that they examined from the Marshall Islands, as did Randall (1955) in the four specimens that he examined from the Gilbert Islands.

CONCLUSION.—*Caranx melampygus* preys on free-swimming fishes and crustaceans, probably most often early and late in the day.

General Remarks on Jacks

Jacks are major predators on many widespread tropical reefs (e.g. Marshall Islands: Hiatt and Strasburg, 1960; Gulf of California: Hobson, 1965, 1968a; Florida Keys: Starck and Davis, 1966; West Indies: Randall, 1967). The larger piscivorous jacks, like *Caranx hippos caninus*, are primarily crepuscular in the Gulf of California (Hobson, 1965, 1968a) and in the Florida Keys (Starck and Davis, 1966).

Family Lutjanidae: snappers

As is true of the sea basses, Hawaiian inshore reefs lack native species of snappers, a family whose members are prominent on shallowwater reefs elsewhere in the tropical Pacific (Gosline and Brock, 1960; Randall and Brock, 1960). Only one species of this family was seen regularly on the Kona study reefs during this project.

Aphareus furcatus (Lacépède)—*gurutsu*

During the day this solitary predator swims slowly, 1 to 2 m above the reef, with never more than a few individuals in any one place. It was not seen at night during this study, perhaps because it avoided our lights. Only once did I see one attack prey: 5 min before sunrise this individual suddenly broke from its patrolling attitude 2 m above the reef and dived among a cluster of small fishes, mostly pomacentrids, that were in the process of emerging from their nocturnal shelters (see Hobson, 1972). The success of the strike was undetermined, but at the instant of attack all small fishes within a radius of about 15 m shot under cover.

Three specimens (253: 244-262 mm) were speared for study. One taken during midafternoon contained a *Plagiotremus goslinei*, a blenny that swims above the reef only in daylight (see account for this species, below); because this prey was relatively fresh, it almost certainly was captured earlier that day. Another *A. furcatus* collected during midafternoon contained moderately digested crab megalops and gammaridean amphipods; although megalops are more typically food of nocturnal predators, the relatively good condition of these small prey indicated they had been collected earlier that day. The third *A. furcatus*, speared during midmorning, was empty. Randall (1955) examined four specimens of this snapper in the Gilbert Islands, and the two with prey contained only fishes.

CONCLUSION.—*Aphareus furcatus* preys on free-swimming fishes and crustaceans during daylight. Its habits at night remain unknown.

General Remarks on Snappers

If *Aphareus furcatus* hunts prey mostly in daylight, it would seem an atypical lutjanid. Generally lutjanids are described as nocturnal fishes (e.g. Hobson, 1965, 1968a: Gulf of California; Starck and Davis, 1966: Florida Keys; Randall, 1967: West Indies).

The efforts that successfully introduced the sea bass *Cephalopholis argus* into Hawaiian waters (see account for that species, above) also included the snapper *Lutjanus vaigiensis*, which now too is well established in Kona. Although *L. vaigiensis* was not numerous in the study area during this work, one school was seen consistently during daylight on irregular visits to a location in Kealakekua Bay, and solitary individuals occasionally were encountered on the reef after dark. Thus, the habits of this fish appear to be similar to those of certain other species of *Lutjanus*

elsewhere; that is, it forms relatively inactive schools during the day, then disperses at nightfall and hunts prey after dark. This pattern is known for *L. argentiventris* in the Gulf of California (Hobson, 1965, 1968a), and for *L. griseus* and others in the tropical Atlantic (Starck and Davis, 1966). Randall and Brock (1960) reported predominantly nocturnal feeding by *L. vaigiensis* in Tahiti and often found this snapper in large aggregations during the day.

Family Sparidae: porgies

Monotaxis grandoculis (Forskål)—*mu*

In Kona, this porgy is most numerous near basalt reefs that are exposed to the prevailing sea. During the day it typically hovers 2 to 3 m above the reef, either in loose aggregations of 4 to 10 fish, or as solitary individuals. When congregated, most individuals display broad bars on their sides dorsally; although this same color pattern occurs frequently in solitary fish, these often are overall pale grey. Those I observed in Kona during the day always seemed inactive; however, Hiatt and Strasburg (1960) reported individuals in the Marshall Islands excavating prey buried in the sand, presumably during daylight. In Kona, *M. grandoculis* disperses from its daytime assemblages at nightfall and forages as solitary individuals throughout the night. After dark, many move into shallower water than is frequented by the species in daylight. The nocturnally active individuals sometimes show the barred color pattern but are most often plain grey (Figure 22).

Of five specimens (312: 244-397 mm) speared during day and night, one that was taken from an aggregation late in the afternoon was empty, whereas all four that were speared at night (later than 4 h after sunset and before first morning light) were full of food, as listed in Table 22.

Although the gut contents were relatively fresh, the shelled items had been reduced to crushed fragments—presumably by the large molarform jaw teeth of this fish.

Prey taken by this porgy in Kona are much the same as taken by the same species in the Marshall Islands (Hiatt and Strasburg, 1960) and Gilbert Islands (Randall, 1955).

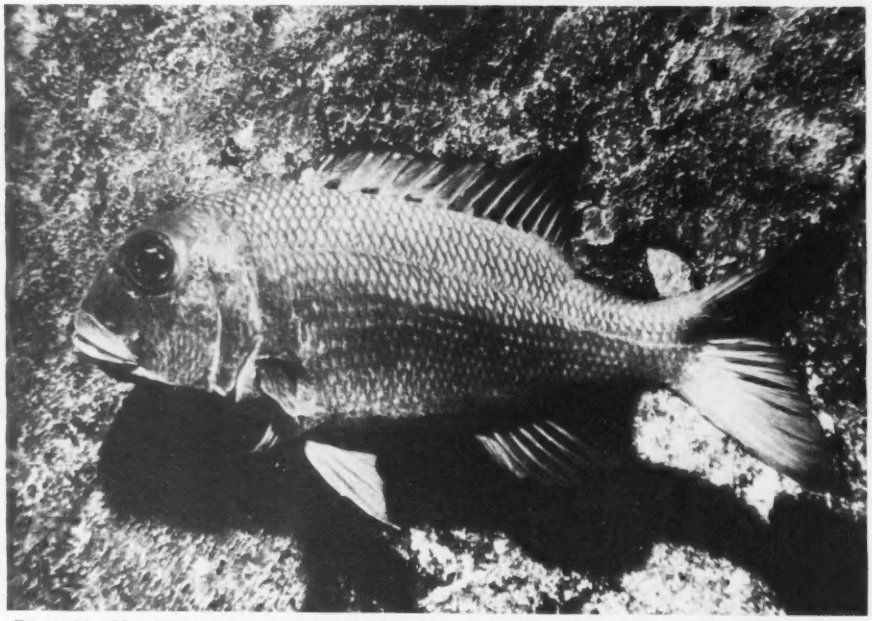

FIGURE 22.—*Monotaxis grandoculis*, a porgy, showing its plain grey coloration as it swims close to the reef at night.

TABLE 22.—Food of *Monotaxis grandoculis*.

Rank	Items	No. fish with this item (n = 4)	Mean percent of diet volume	Ranking index
1	Prosobranch gastropods	4	21.3	21.30
2	Ophiuroids	3	27.1	20.33
3	Echinoids	3	21.3	15.98
4	Opisthobranch gastropods	2	11.8	5.90
5	Pagurid crabs	2	3.8	1.90
6	Polychaetes	1	3.8	0.95
7	Brachyuran crabs	1	2.5	0.63
8	Tunicates	1	2.5	0.63
9	Egg masses (unident.)	1	1.3	0.33
10	Holothurians	1	0.8	0.20
Also, crustacean fragments		1	2.5	0.63
	Algal fragments	1	1.3	0.33

CONCLUSION.—*Monotaxis grandoculis* is a nocturnal predator that feeds on benthic invertebrates, most of them heavily shelled.

General Remarks on Porgies

Porgies are closely related to the snappers, most of which seem to be mainly nocturnal. Nevertheless, porgies have been reported as diurnal, for example species of *Archosargus, Diplodus,* and *Calamus* in the tropical Atlantic (Randall, 1967). Still, Starck and Davis (1966) recognized that species of *Calamus* in Florida may also feed at night. Diurnal habits in porgies may be attributed to their habit of excavating buried prey, which makes available to them certain nocturnal forms that have concealed themselves in the sand during daylight.

Family Mullidae: goatfishes

Mulloidichthys auriflamma (Forskål)—*weke'ula*

During the day this goatfish, which is relatively numerous in Kona, hovers in schools above the reef, or (occasionally) under ledges. Individuals recognized by distinguishing marks occurred in schools at the same locations each day, even though these schools disperse at nightfall. After dark, solitary or in small groups, this species probes with its barbels in the sandy areas adjacent to the reef, and in some of the larger sand patches on the reef. When illuminated by a diving light at night, it often shows a deep reddish hue that seems to be a reaction to the light, not a nocturnal coloration.

Of the 22 individuals (170: 110-235 mm) speared during day and night, all 12 collected from schools during the afternoon were either empty or contained only well-digested fragments, whereas of the 10 collected at night (later than 3 h after sunset and before sunrise), all contained food, including fresh material, as listed in Table 23.

Thus my observations concur with those of Gosline and Brock (1960), who reported that *M. auriflamma* does not feed during the day, but instead schools quietly in certain established areas and then disperses to forage at night.

Although crab megalops, a primary food, are a major element of the plankton, most of those captured by this goatfish probably were taken from the sand.

CONCLUSION.—*Mulloidichtys auriflamma* is a nocturnal predator that feeds on invertebrates that live in the sand.

Mulloidichthys samoensis (Günther)—*weke 'a'a*

This goatfish, widespread in Kona, often hovers in quiet schools over the reef during the day, where it looks much like *M. auriflamma,* above. Although *M. samoensis* is a more elongated fish, the two must be seen together before this distinction is obvious. Sometimes the two species school together, but more often they are segregated. Frequently instead of schooling during the day, *M. samoensis,* but not *M. auriflamma,* moves as solitary individuals or in small groups over sand patches on the reef, and there actively probes with its barbels in the sediment. These active individuals have a color pattern distinct from that of relatively inactive conspecifics in schools. When schooling, *M. samoensis* has a prominent yellow stripe running from eye to tail along its upper sides, as does *M. auriflamma* in similar schools (Figure 23a); however, this stripe is not present (or at least is indistinct) when *M. samoensis* actively

TABLE 23.—Food of *Mulloidichthys auriflamma*.

Rank	Items	No. fish with this item (n = 10)	Mean percent of diet volume	Ranking index
1	Crab megalops	6	11.5	6.90
2	Ophiuroids	4	14.5	5.80
3	Polychaetes	4	11.7	4.68
4	Xanthid crabs	6	7.0	4.20
5	Prosobranch gastropods	7	4.7	3.29
6	Echinoids	6	4.7	2.82
7	Gammaridean amphipods	5	1.3	0.65
8	Isopods	4	1.1	0.44
9	Ostracods	2	0.6	0.12
10	Sipunculid introverts	1	0.5	0.05
11	Pelycypods	1	0.5	0.05
12	Penaeid shrimps	1	0.5	0.05
13	Portunid crabs	1	0.2	0.02
Also, crustacean fragments		4	8.5	3.40
	Unidentified fragments	2	12.0	2.40
	Algal fragments	1	1.0	0.10
	Sand, foraminiferans, and debris	7	19.7	13.79

forages on the reef, it being replaced by a black spot on the fish's side, below the dorsal fin (Figure 23b).

At nightfall, those individuals of *M. samoensis* that had been hovering over the reef in quiet schools disperse. After dark the species not only continues the activity that some members had pursued over reef sand patches in daylight, but also extends this activity in some areas farther out over the more extensive sandy areas adjacent to the reef. When illuminated by a light at night, *M. samoensis* frequently displays a color pattern of red blotches that seems to be a response to the light, rather than being a nocturnal color feature. Its coloration at night is as described above for foraging individuals in daylight. After a night of foraging, many individuals regroup in the morning, forming schools that reappear in the same locations each day.

Twenty-three specimens (182: 136-283 mm) were speared during day and night. Of four taken during afternoons as they probed sand patches on the reef, swimming in small groups or as individuals, two had full stomachs that included relatively fresh prey; the other two contained only debris. Of three individuals taken while they hovered in schools over the reef during the afternoon, one had an empty stomach, and the other two contained only well-digested fragments. Contrasting data were provided by 16 specimens speared as they actively probed in sand patches on the reef during the 2 h immediately before first morning light, and during the first 30 min of morning twilight. Of these, 11 had full stomachs, including much fresh material, 2 contained only bits of debris, and only 3 were empty. Items in the 13 individuals containing identifiable prey are listed in Table 24.

No obvious difference was noted between prey taken during day and night although pertinent data are too few for meaningful comparison. Hiatt and Strasburg (1960) reported that fishes are an important food of this goatfish in the Marshall Islands. Otherwise, they listed foods similar to those taken by the species in Kona.

CONCLUSION.—*Mulloidichthys samoensis* preys on sand-dwelling invertebrates, mostly at night, but to some extent during the day.

Parupeneus multifasciatus (Quoy and Gaimard) —*moano*

This is the most numerous and widespread goatfish on Kona reefs. During the day solitary individuals and groups of two or three actively probe with their barbels among cracks and crevices on the reef, especially in pockets where sand and debris have accumulated. This species is active through twilight, but generally appears inactive after dark, when solitary individuals rest in exposed locations on the reef. To some extent these immobile nocturnal attitudes may be influenced by the diving light, but not to the extent indicated for *P. bifasciatus*, below; certainly the blotched red color pattern often displayed at this time is a reaction to the light. On nights of bright moonlight, at least some individuals of *P. multifasciatus* swim over the reef.

Thirty specimens (162: 125-212 mm) were speared during day and night. Of 14 collected during the hour immediately before first morning

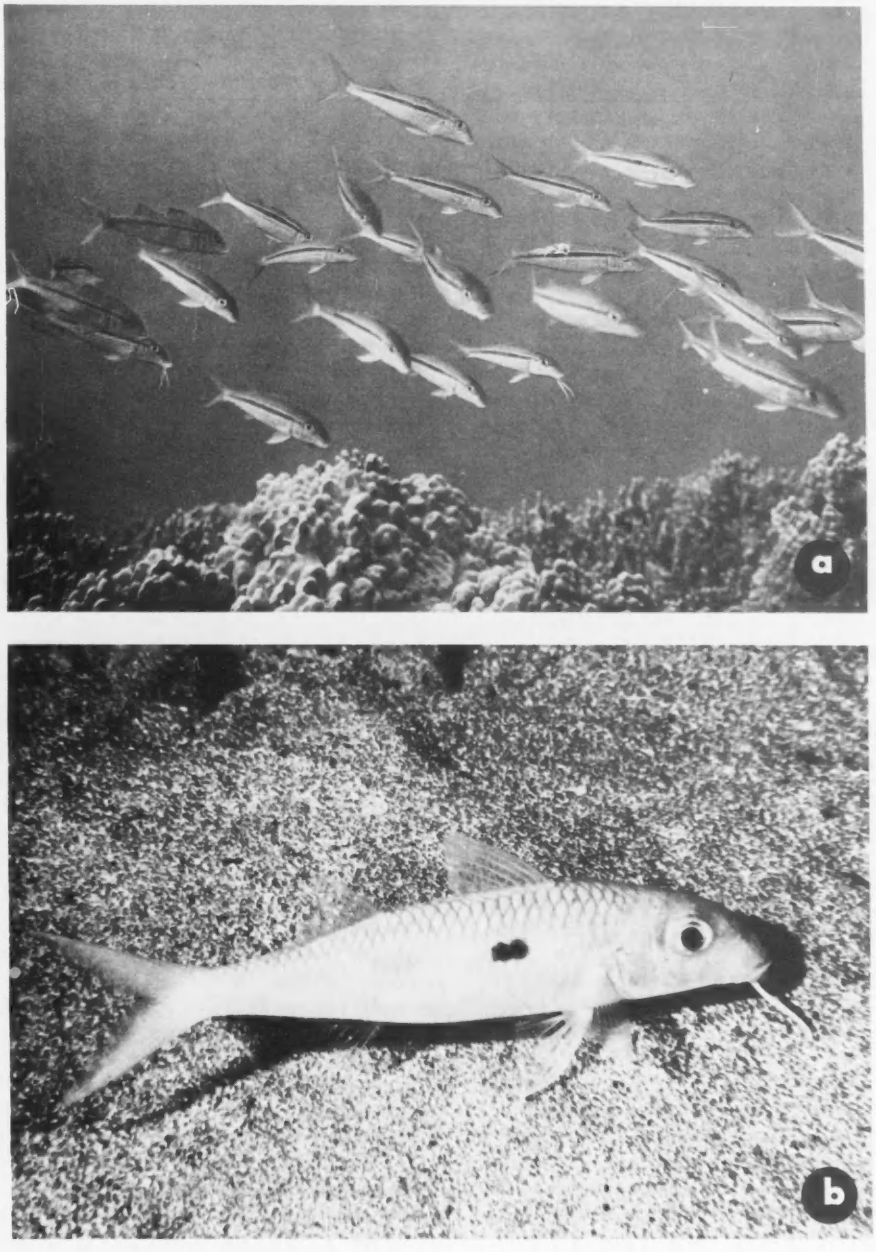

FIGURE 23.—*Mulloidichthys samoensis*, a goatfish: a, with the coloration shown when schooling during the day; b, with the coloration shown when feeding as a solitary individual or in small groups during both day and night.

TABLE 24.—Food of *Mulloidichthys samoensis*.

Rank	Items	No. fish with this item (n = 13)	Mean percent of diet volume	Ranking index
1	Pelecypods	7	10.0	5.39
2	Polychaetes	5	11.2	4.31
3	Gammaridean amphipods	7	6.7	3.61
4	Prosobranch gastropods	6	3.1	1.43
5	Sipunculid introverts	3	5.4	1.25
6	Crab megalops	3	3.1	0.72
7	Isopods	3	2.8	0.65
8	Hippid crabs	1	0.8	0.06
9	Echinoids	1	0.8	0.06
10	Xanthid crabs	1	0.4	0.03
11	Shrimps	1	0.2	0.02
Also, crustacean fragments		5	7.1	2.73
	Unidentified fragments	3	11.6	2.68
	Sand and debris, including foraminiferans	13	36.8	36.80

TABLE 25.—Food of *Parupeneus multifasciatus*.

Rank	Items	No. fish with this item (n = 18)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	14	30.6	23.80
2	Caridean shrimps	8	15.4	6.84
3	Crab megalops	5	8.6	2.39
4	Prosobranch gastropods	3	1.8	0.30
5	Tanaids	2	0.6	0.07
6	Gammaridean amphipods	2	0.4	0.04
7	Stenopid shrimps	1	0.6	0.03
8	Ostracod	1	0.1	0.01
Also, crustacean fragments		14	29.4	22.87
	Unidentified fragments	1	0.8	0.04
	Debris	7	11.7	4.55

light, and through morning twilight, the stomachs of 12 were empty, but the other 2 contained prey in varying stages of digestion that appeared to have been taken during the night (one night with, the other without, moonlight). In contrast, all 16 specimens speared on the reef during the afternoon contained prey in varying stages of digestion, including fresh material. Items in the 18 containing identifiable material are listed in Table 25.

No obvious difference in diet was noted between the 2 individuals of *P. multifasciatus* that apparently had captured their prey at night and the 14 that had been feeding in daylight; however, the data are too few for a meaningful comparison.

Juveniles of *P. multifasciatus* sometimes aggregate up in the water column where plankton abounds, apparently feeding on these organisms, but none of these individuals were collected. The relatively high incidence of crab megalops in the diet of this and other bottom-feeding goatfishes may reflect some predation on free-swimming forms in the water column, but I believe that at least most of these megalops were taken off the sea floor.

CONCLUSION.—*Parupeneus multifasciatus* is primarily a diurnal predator that takes benthic crustaceans.

Parupeneus bifasciatus (Lacépède)—*munu*

This goatfish, which exceeds 300 mm when fully grown, is especially numerous among basalt boulders—frequently solitary, but also in groups of two or three. In daylight, its actions appear much like those of *P. multifasciatus*, which it resembles, but after dark, when *P. multifasciatus* generally rests on the reefs, *P. bifasciatus* usually moves about. Nevertheless, when *P. bifasciatus* is illuminated by the diving light it often settles immobile onto the reef—an action that complicates assessing its nocturnal activity. Like *P. multifasciatus*, *P. bifasciatus* often displays at this time a blotched red-colored pattern that seems to be a response to the diving light.

Twenty-seven specimens (229: 164-300 mm) were speared during day and night. Of 11 taken as they swam close to the reef during early morning (between first light and 3 h after sunrise), the stomachs of 2 were empty, but the other 9 contained prey in varying stages of digestion, some of

it fresh. Similarly, of 12 individuals collected as they swam close to the reef during afternoons, only 1 had an empty stomach, whereas the other 11 contained prey in varying stages of digestion, some of it fresh. Finally, of four specimens speared at night (between 4 and 5 h after sunset) the stomach of one was empty, but the other three contained prey in varying stages of digestion, some of it fresh.

These data indicate that *P. bifasciatus* feeds regularly during both day and night. Recognizing that the contrasting conditions under which it hunts may be reflected in the composition of its diet, I attempted to distinguish prey that had been taken by day from that taken at night. Although, undoubtedly there is overlap, generally specimens collected during the night and early morning should contain mostly prey captured after dark, whereas specimens taken during afternoons should contain mostly prey taken in daylight.

Thus, the 12 *P. bifasciatus* taken during the night and early morning with identifiable material in their stomachs presumably represent mostly nocturnal feeding. Items in these individuals are listed in Table 26. Using the same rationale, diurnal feeding presumably is reflected in the 11 *P. bifasciatus* collected with identifiable material in their stomachs during afternoons. Items in these individuals are listed in Table 26.

Although xanthid crabs are the major prey day and night, they assume greater relative importance in daylight, as do caridean shrimps. Xanthids and carideans are largely under cover in daylight, where they may be especially vulnerable to this predator's probing actions. Crab megalops become increasingly important to this goatfish at night, but the circumstances surrounding their capture remain uncertain; megalops are the major prey of many nocturnal planktivores, such as *Myripristis* spp. (see accounts for these species, above), but are also taken day and night by predators like certain goatfishes that probe the sea floor.

Based on the above data, fishes seem to be more available as prey to *P. bifasciatus* at night. Prey fishes that could be identified were blennies and pomacentrids, which are diurnal fishes that take cover after dark. Apparently *P. bifasciatus* is adapted to capture these resting diurnal fishes at night, but is less effective in capturing the fishes that are under cover during daylight.

CONCLUSION.—*Parupeneus bifasciatus* hunts prey on the reef during both day and night. Adult crabs and shrimps are more important as prey during the day than at night, whereas the reverse is true of fishes and crab megalops.

Parupeneus porphyreus (Jenkins)—*kumu*

This is the most numerous goatfish on some Hawaiian reefs (Gosline and Brock, 1960), but

TABLE 26.—Food of *Parupeneus bifasciatus*.

Nighttime Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	10	29.0	24.17
2	Fish	6	17.0	8.50
3	Crab megalops	5	19.4	8.08
4	Caridean shrimps	7	8.0	4.67
5	Octopods	2	3.9	0.65
6	Oxyrhynchid crabs	2	1.7	0.28
7	Prosobranch gastropods	2	0.6	0.10
8	Polychaetes	1	0.4	0.03
9	Gammaridean amphipods	1	0.3	0.03
Also, crustacean fragments		7	15.5	9.04
	Debris	2	4.2	0.70

Daytime Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	9	43.3	35.43
2	Caridean shrimps	9	15.5	12.68
3	Crab megalops	3	3.5	0.95
4	Octopods	1	7.1	0.65
5	Grapsid crabs	1	3.9	0.35
6	Oxyrhynchid crabs	1	1.1	0.10
7	Fish	1	0.7	0.06
8	Gammaridean amphipods	2	0.2	0.04
Also, crustacean fragments		8	24.7	17.96

there are relatively few in the Kona study area. During the day this species stays close to cover, where it usually occurs in small groups under ledges. At night solitary individuals are active close among rocks and coral on the reef.

Of the 11 specimens (157: 137-173 mm) collected, 6 speared close to reef crevices late in the afternoon either were empty or contained only a few well-digested fragments, whereas all 5 collected in the same places within 1 h after sunrise had stomachs full of prey, some of it fresh, as listed in Table 27.

CONCLUSION.—*Parupeneus porphyreus* is a nocturnal predator that feeds mostly on benthic crustaceans.

Parupeneus chryserydros (Lacépède)—*moano kea*

The scientific name of this goatfish remains uncertain. I follow Gosline and Brock (1960) in recognizing the nominal *P. chryserydros*, even though some authors (e.g. Lachner, 1960) refer this form to *P. cyclostomus* (Lacépède). Growing to about 600 mm long (Gosline and Brock, 1960), *P. chryserydros* is the largest of the goatfishes occurring regularly on Kona reefs.

During the day, solitary individuals or groups of two to five move over the reef, where their exceptionally long barbels work through the covering on rocky substrata. More often than not, groups of *P. chryserydros* are accompanied by a single jack, *Caranx melampygus*, which follows close behind them. For 1 mo I recorded all sightings of *P. chryserydros* that swam in groups of two or more, and of 24 such groups, 16 were accompanied by a jack. Usually solitary individuals of this goatfish are not thus accompanied, but this too was seen four times during the month. Clearly, it is the jack that maintains the association, probably as a tactic to capture prey driven from cover as the foraging goatfish disturb the substratum. Apparently the jack finds this advantage only with *P. chryserydros*, as it was not seen similarly following other species. Titcomb and Pukui (1952) listed many ancient Hawaiian fish names which they were unable to associate with species recognized today. One of these, *moano ukali ulua*, translates as "moano with ulua following," and probably refers to *P. chryserydros*. Whereas the adults of *P. chryserydros* are followed by the jack, the juveniles of this goatfish frequently swim close beneath various labrids, especially *Thalassoma duperrey*, and here it is the goatfish that maintains the associations, though to what advantage I do not know.

Of the 20 specimens (261: 123-363 mm) collected, all 3 that were speared as they rested on the reef at night (between 4 h after sunset and first morning light) had empty guts, whereas 15 of 17 taken as they swam close to the reef at various times of the day (between midmorning and late afternoon) had prey in their stomachs, and only the other 2 were empty.

Fish were the major item, occurring in 13 of the 15 individuals that contained food (mean percent of diet volume: 83.1; ranking index: 72.02). Other food items were: xanthid crabs in two individuals (mean percent of diet volume: 8.3; ranking index: 1.11), caridean shrimps in one (mean percent of diet volume: 1.3; ranking index: 0.09), and unidentified fragments in two (mean percent of diet volume: 7.3; ranking index: 0.97).

The fishes in the diet ranged between 25 and 102 mm long, and included the following species: *Abudefduf imparipennis* (1), *Cirrhitops fasciatus* (2), *Istiblennius gibbifrons* (1), *Plagiotremus goslinei* (1), *Cirripectus* sp. (4), and a labrid (1). All of these are diurnal fishes that swim close to the reef in daylight, but take cover when a predator approaches. Judging by how *P. chryserydros* feeds,

TABLE 27.—Food of *Parupeneus porphyreus*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	5	65.2	65.20
2	Hippid crabs	1	10.0	2.00
3	Caridean shrimps	1	2.0	0.40
4	Prosobranch gastropods	1	0.2	0.04
5	Chitons	1	0.2	0.04
6	Gammaridean amphipods	1	0.2	0.04
Also,	crustacean fragments	3	21.2	12.72
	Debris	1	1.0	0.20

small fishes that have taken shelter on its approach probably are detected and even driven out from under cover by the exceptionally long barbels of this goatfish. If the probing barbels do in fact drive small fishes from their hiding places, this would account for the behavior of the jacks that follow them, described above. These same prey fishes also shelter themselves at night when they are inactive, so one might ask why this goatfish does not hunt for them at that time too. As reported above, *P. bifasciatus* preys on some of these same fishes (pomacentrids and blennies) when they are inactive under shelter at night. But capturing a relatively inert diurnal fish that is resting under cover after dark probably presents different problems for a predator than capturing an alert fish that has taken refuge from some specific threat in daylight. It appears that *P. bifasciatus* is adapted to taking these fishes when they rest under cover at night, whereas *P. chryserydros* is adapted to take them when they seek shelter in daylight. After dark, *P. chryserydros* is inactive, resting under reef cover (Figure 24).

Parupeneus cyclostomus in the Marshall Islands, which is closely related to *P. chryserydros*, if not conspecific, was reported by Hiatt and Strasburg (1960), on the basis of 16 specimens, to be an "active feeder on small benthonic fishes," but may prey more heavily on crustaceans than does the Hawaiian form.

CONCLUSION.—*Parupeneus chryserydros* is a diurnal predator that feeds mostly on small fishes.

General Remarks on Goatfishes

Despite their superficial similarity, the various goatfishes behave distinctively. Some, such as *Mulloidichthys auriflamma* and *Parupeneus porphyreus*, are primarily nocturnal; others, including *P. chryserydros* and *P. multifasciatus*, are mostly diurnal; and still others, like *P. bifasciatus* and *M. samoensis*, regularly hunt prey during both day and night. One might suppose that fishes which probe the sea floor for food would be indifferent to changes associated with day and night, but obviously this is not so. Whether a given species of goatfish is primarily diurnal or nocturnal probably relates to the differential day-night habits of its specific prey. That some goatfishes are

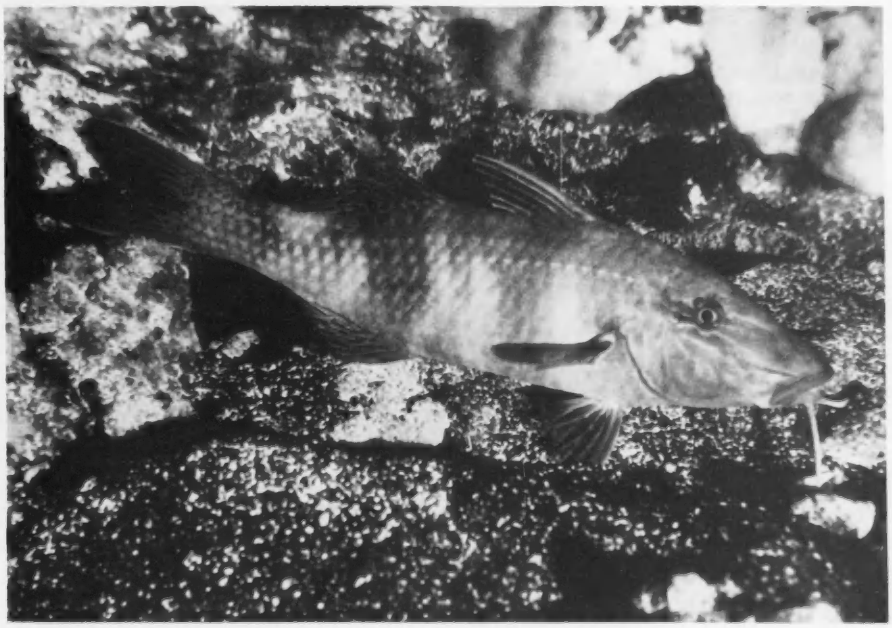

FIGURE 24.—*Parupeneus chryserydros*, a goatfish, resting under a ledge at night, with its exceptionally long chin barbels spread out before it.

nocturnal, whereas other are diurnal, is also recognized from other seas. In Florida, Starck and Davis (1966) suspected that *Mulloidichthys martinicus* feeds at night, whereas they recognized diurnal feeding habits in *Pseudupeneus maculatus*. Longley and Hildebrand (1941), as well as Collette and Talbot (1972), also regarded *M. martinicus* as nocturnal and *P. maculatus* as diurnal. Randall (1967) reported that *M. martinicus* feeds by day as well as night, and described a diet much like that of the two species of *Mulloidichthys* from Kona.

Family Kyphosidae: sea chubs

Kyphosus cinerascens Forskål—*nenue*

In Kona, *K. cinerascens* is most numerous where a basalt reef face confronts the prevailing swell in water deeper than about 8 m. Often over 500 mm long, this fish is active throughout the day—usually in groups of up to 10 or more individuals, and often swimming high in the water column. At night, solitary individuals swimming above the sea floor are often encountered in the same areas.

All three specimens (205: 166-250 mm) collected for study had guts full of a wide variety of benthic algae exclusively. Although two of these fish were taken during midday, the other was taken at night, within 1 h before first morning light. No sedimentary material was mixed in these gut contents, indicating that the algae had been bitten, not scraped, off the rocks, or else had been taken as fragments drifting in mid-water. Hiatt and Strasburg (1960) found the same gut contents in specimens from the Marshall Islands.

CONCLUSION.—*Kyphosus cinerascens* feeds during the day, cropping algae from rocks or taking them as drifting algal fragments. Its nocturnal habits remain uncertain.

General Remarks on Sea Chubs

Sea chubs generally are described as diurnal herbivores (e.g. Longley and Hildebrand, 1941; Starck and Davis, 1966; Randall, 1967). Smith (1907) reported crabs and bivalved mollusks among algae in the diet of *Kyphosus sectatrix* in the Atlantic Ocean, but these items probably were taken incidentally with the algae. Randall (1967) found only algae and a bit of sea grass in *K. sectatrix* from the West Indies. Starck and Davis (1966) reported that *K. incisor* rests in sheltered locations on Floridian reefs at night after having fed on drifting sargassum at the water's surface during the day. In the East Indies, however, William N. McFarland, Cornell University (pers. commun.) observed kyphosids active at night.

Family Chaetodontidae: angelfishes and butterflyfishes

The chaetodontids comprise two distinct groups: the angelfishes, subfamily Pomacanthinae; and the butterflyfishes, subfamily Chaetodontinae. Of the species treated below, the first two are angelfishes, the remainder are butterflyfishes.

Holacanthus arcuatus Gray—angelfish

This angelfish is sparsely distributed on Kona reefs, but being relatively large and distinctive is readily noticed where it occurs. Usually solitary or paired, it swims close among rock ledges and boulders at depths below about 8 m. During the day it picks material from the surface of rocks, but was not seen active at night.

Six specimens (136: 123-150 mm) were speared during afternoons, and all had full stomachs. They had fed almost exclusively on sponges (mean percent of diet volume and ranking index: 98.3). The only other items—algae and hydroids—probably were taken incidentally with the sponges.

CONCLUSION.—*Holacanthus arcuatus* is a diurnal species that feeds on sponges.

Centropyge potteri (Jordan and Metz)—potter's angelfish

An abundant species in coral-rich surroundings, this small angelfish behaves more like some of the damselfishes than it does other members of its family. A given individual limits its movements to restricted, well-defined locations close among fingerlike growths of the coral *Porites compressus*. During the day it swims about, picking at material growing over dead coral. At night it is alert, but secreted deep among the coral, apparently inactive.

All five specimens (80: 69-86 mm long) speared at various times during the day were full of food. Filamentous algae were the major identifiable item in the gut contents of all five (mean percent of

diet volume and ranking index: 41.7). There also was much unidentified debris, including sand and foraminiferans (mean percent of diet volume and ranking index: 42.3) that all five apparently had scraped from the substratum, and which probably included substantial nourishment in the form of organic detritus. The other components of the diet, all minor, were: diatoms in all five (mean percent of diet volume and ranking index: 3.3), sponges in all five (mean percent of diet volume and ranking index: 2.3), and harpacticoid copepods in one (mean percent of diet volume: 0.3; ranking index: 0.06).

CONCLUSION.—*Centropyge potteri* is a diurnal species that feeds on benthic algae and probably on organic detritus.

Forcipiger flavissimus Jordan and McGregor—*lau wiliwili nukunuku 'oi 'oi*

This long-snouted species (Figure 25a), numerous in Kona, and widespread throughout the Indo-Pacific region, was long called *F. longirostris*. Only recently has the distinction between *F. flavissimus* and the true *F. longirostris* (Figure 25b and c; treated below) been recognized (Wheeler, 1964; Randall and Caldwell, 1970). *Forcipiger flavissimus* occurs singly, or, more often, in groups of two or three. It is active throughout the day, especially over coral-rich reefs, where it picks at objects on a variety of surfaces. At night it is alert close among rock and coral cover but apparently inactive.

Twenty-seven specimens (116: 94-137 mm) were speared during day and night. Of 11 that were taken either at night (later than 4 h after sunset) or during early morning twilight, the stomachs of 9 were empty, and those of 2 (collected between 4 and 5 h after sunset) contained only a few well-digested fragments. In contrast, all 16 specimens taken at various times of the day had full stomachs, including relatively fresh material, as listed in Table 28.

Most of the unidentified fragments among the gut contents were relatively fresh pieces that this fish apparently had recently torn from the bodies of larger animals. The similarity of its elongated snout and mouth to a pair of needle-nosed pliers (Figure 26, lower) underscores the adaptiveness of its feeding apparatus to this habit. Even the gripping surfaces on the pliers are paralleled in the snout of *F. flavissimus* by expanded contact-surfaces in both upper and lower jaws—both of which carry multiple rows of short, inwardly curving teeth (Figure 27b).

CONCLUSION.—*Forcipiger flavissimus* is a diurnal predator that tears pieces off larger benthic animals.

Forcipiger longirostris (Broussonet)—*lau wiliwili nukunuku 'oi 'oi*

This species is relatively numerous in Kona, although it appears to be rare elsewhere in Hawaii. Both color varieties—the yellow form (Figure 25b), which is essentially identical to *F. flavissimus*, discussed above, and the dark brown form (Figure 25c)—were observed regularly throughout the study. Like *F. flavissimus*, *F. longirostris* occurs typically over coral-rich reefs, and the two species overlap extensively; however, in areas where one is numerous, the other occurs less frequently. Despite this, I was unable to relate observed differences in relative numbers to specific habitat differences. *Forcipiger longirostris* is generally larger, but the most obvious morphological distinction between the two lies in the relative lengths of their snouts and in their different mouth structures (Figure 26). Less noticeable, but probably also related to feeding, *F. longirostris* has relatively larger eyes. Like its congener, *F. longirostris* is active on the reef by day, swimming singly or in groups of two or three, and probing with its long snout in cracks and crevices. At night it is close among cover of rocks or coral—alert, but apparently inactive.

Of the 26 specimens (136: 98-162 mm) collected, all 4 that were speared at night (later than 4 h after sunset and before first light in the morning) had empty stomachs, whereas the stomachs of all 22 collected at various times during the afternoon were full (including relatively fresh items). Decapod shrimps were the major prey, occurring in all 22 individuals that contained food (mean percent of diet volume and ranking index: 88.4). Other food items were: pagurid crabs, without the mollusk shell, in two individuals (mean percent of diet volume: 1.9; ranking index: 0.17), fish fragments in one (mean percent of diet volume: 0.5; ranking index: 0.02), and crustacean fragments in nine (mean percent of diet volume: 9.2; ranking index: 3.76).

In contrast to the omnivorous *F. flavissimus*, *F. longirostris* has a restricted diet. It does not tear

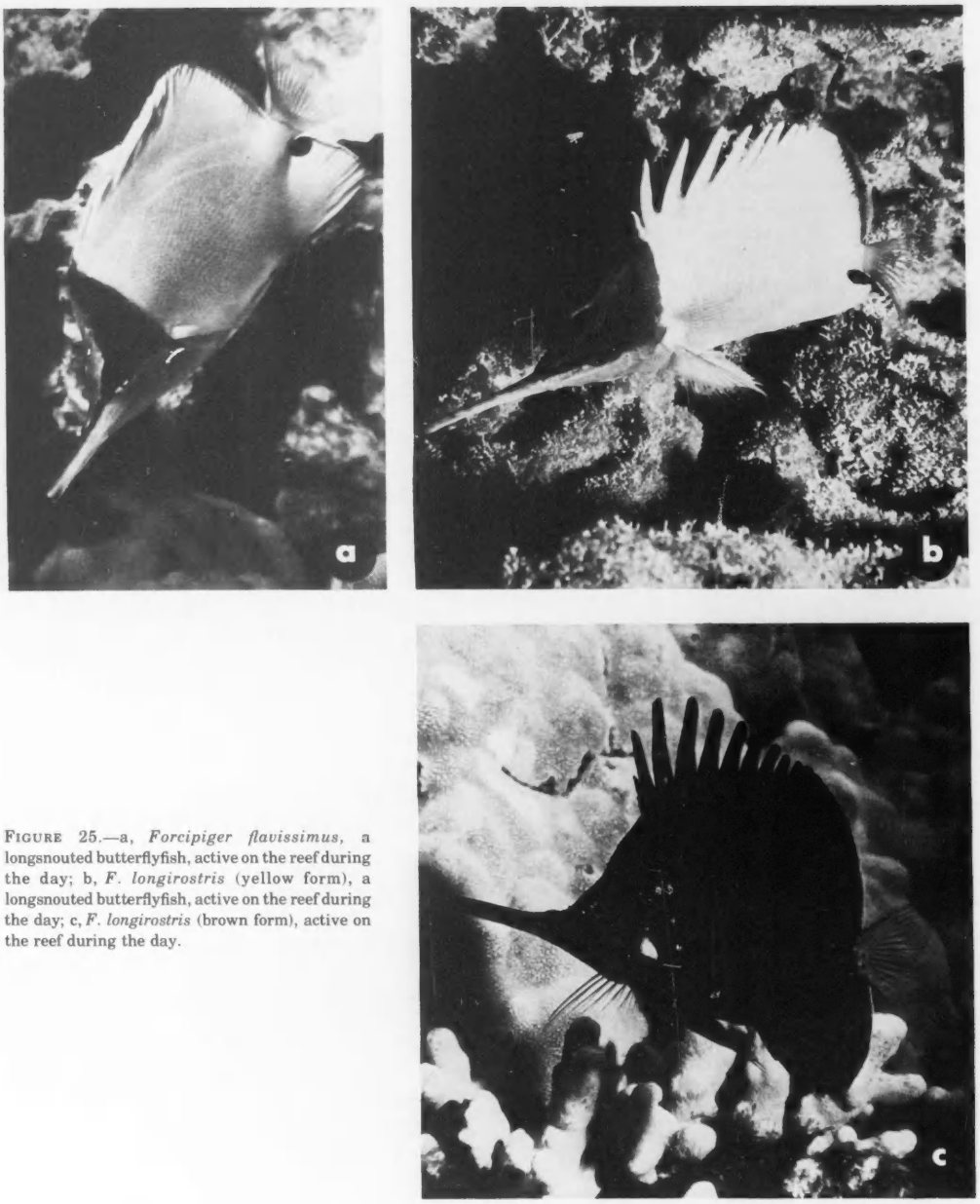

FIGURE 25.—a, *Forcipiger flavissimus*, a longsnouted butterflyfish, active on the reef during the day; b, *F. longirostris* (yellow form), a longsnouted butterflyfish, active on the reef during the day; c, *F. longirostris* (brown form), active on the reef during the day.

TABLE 28.—Food of *Forcipiger flavissimus*.

Rank	Items	No. fish with this item (n = 16)	Mean percent of diet volume	Ranking index
1	Radioles of sabellid polychaetes	10	15.4	9.63
2	Nemerteans	7	11.9	5.21
3	Podia and pedicellaria of echinoids	9	7.0	3.94
4	Calanoid copepods	8	4.1	2.05
5	Tentacles of terebellid polychaetes	7	3.6	1.58
6	Gammaridean amphipods	7	2.3	1.01
7	Hydroids	8	1.0	0.50
8	Caridean shrimps	2	1.3	0.16
9	Caprellid amphipods	4	0.5	0.13
10	Sipunculid introverts	3	0.6	0.11
11	Prosobranch gastropod egg capsules	3	0.5	0.09
12	Crab megalops	2	0.1	0.01
13	Isopods	1	0.1	<0.01
14	Demersal fish eggs	1	0.1	<0.01
Also, crustacean fragments		2	0.9	0.11
	Algal fragments	2	0.2	0.03
	Unidentified fragments	15	50.4	47.25

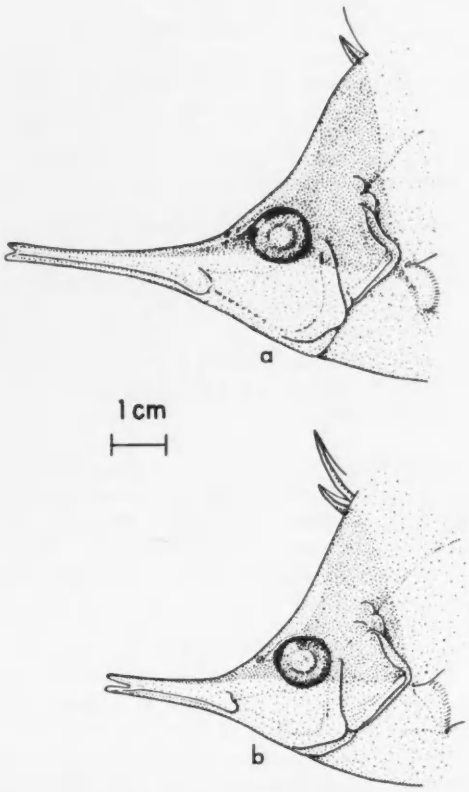

FIGURE 26.—The head and snout of: a, *Forcipiger longirostris*, 102mm long; *F. flavissimus*, 103 mm long. (Note: to discount the size difference in their snouts, lengths were measured from the posterior edge of the maxillary.)

off pieces of larger organisms, as does its congener, but instead takes only whole prey. The sharp difference between their diets is reflected in differing feeding structures. The snout and mouth of *F. longirostris* do not suggest needle-nosed pliers, as do those of *F. flavissimus;* indeed, for *F. longirostris,* the generic name *Forcipiger* (from the Latin *forcipis,* meaning pincers) is a misnomer. Compared with *F. flavissimus,* the mouth of *F. longirostris* is smaller and its jaws do not have the greatly expanded contact surfaces; the teeth are inwardly curved, as in *F. flavissimus,* but are longer and confined to only two or three rows at the front of the mouth (Figure 27a). Clearly, *F. longirostris* is adapted to grasping the tiny prey on which it feeds, but not to tearing pieces free.

CONCLUSION.—*Forcipiger longirostris* is a diurnal predator that takes small benthic animals, mostly decapod shrimps.

Hemitaurichthys thompsoni Fowler

This plain dark-brown chaetodontid seems to be generally rare in Hawaii (Gosline and Brock, 1960), but is numerous in several locations near

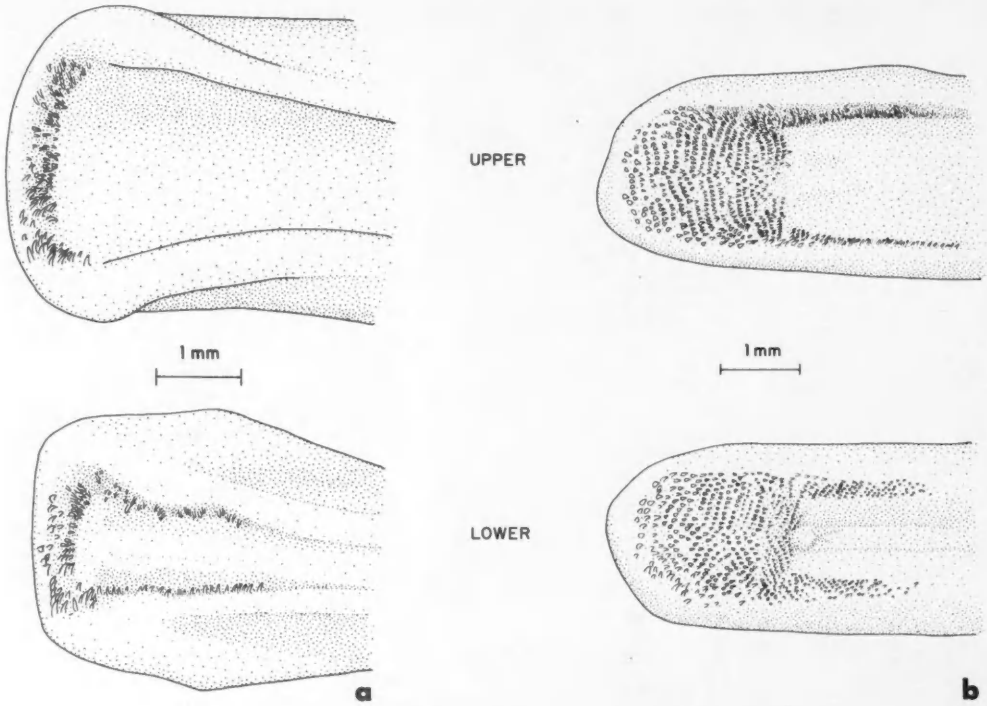

FIGURE 27.—Dentition of: a, *Forcipiger longirostris*; b, *F. flavissimus*.

the outer drop-off at Puuhonua Point, Honaunau. During the day it is active in large aggregations high in the water column, but at nightfall descends to the reef and remains close among cover until morning.

Of the 11 specimens (167: 127-185 mm) collected, all 5 that were taken from under cover on the reef at night (between 4 h after sunset and daybreak) had empty guts, whereas all 6 taken during afternoons from aggregations in midwater were full of food, as listed in Table 29.

I saw no evidence of benthic feeding by this fish. The circumstance that various planktonic copepods made up over 86% of its diet indicates that *H. thompsoni* is a more specialized feeder than its congener *H. zoster* below.

TABLE 29.—Food of *Hemitaurichthys thompsoni*.

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	6	81.9	81.90
2	Blue-green algae in gelatinous sacs	4	3.5	2.33
3	Cyclopoid copepods	4	3.5	2.33
4	Fish eggs, planktonic	4	1.0	0.67
5	Harpacticoid copepods	4	0.7	0.47
6	Hyperiid amphipods	3	0.3	0.15
7	Gastropods, planktonic	1	0.3	0.05
8	Unidentified egg masses in gelatinous matrix	1	0.2	0.03
9	Mysids	1	0.2	0.03
10	Larvaceans	1	0.2	0.03
Also, unidentified fragments		4	8.2	5.47

CONCLUSION.—*Hemitaurichthys thompsoni* is a diurnal planktivore that takes mostly copepods.

Hemitaurichthys zoster (Bennett)—blackface butterflyfish

Gosline and Brock (1960) stated that the colorful *H. zoster* (Figure 28a) and *H. thompsoni* attain a similar size (about 175 mm), but of those seen during this project, *H. zoster* was consistently smaller. Of the two, *H. zoster* also was by far the more numerous and more widespread. During the day *H. zoster* aggregates much like *H. thompsoni*, especially where the reefs drop abruptly into water deeper than about 10 m. Where *H. thompsoni* occurred, *H. zoster* was always nearby, but mixed aggregations of the two species were never seen. Unlike *H. thompsoni*, which was seen feeding only in mid-water, *H. zoster* sometimes is active in small groups close to the reef. At night *H. zoster* is generally solitary, close among cover in the same areas where it is active in daylight. Although *H. thompsoni* has the same coloration day and night, *H. zoster* displays a color pattern at night that differs strikingly from its daytime coloration (Figure 28a and b).

Twelve specimens (119: 100-128 mm) were collected during day and night. Four were speared during morning twilight from a group milling about close above the reef just prior to rising into mid-water. Two of these, taken 18 and 20 min before sunrise, respectively, both had empty stomachs; the third, taken 15 min before sunrise, contained calanoid copepods in varied stages of digestion; the fourth, taken 10 min before sunrise, contained more than 100 calanoid copepods and assorted other prey in varied stages of digestion. I cannot believe that all these prey had been taken since first light that morning, especially as no feeding was observed, and these fish had not yet risen to their customary plankton-feeding levels. And yet *H. zoster* was never seen above the reef at night. Until additional data are available, these two specimens remain anomalous. The other eight specimens, taken at various times during daylight from small aggregations above the reef, all had full stomachs. Items in the 10 individuals containing identifiable prey are listed in Table 30.

These data indicate that *H. zoster* has feeding habits that are less specialized than those of *H. thompsoni*. Planktonic copepods, constituting almost 62% of its diet, are still the major prey, but are less dominant than in *H. thompsoni*. Furthermore, *H. zoster* appears to feed significantly on benthic prey: the alcyonarian *Sarcothelia edmondsoni* constituted over 60% of the material in each of the three specimens in which it occurred.

CONCLUSION.—*Hemitaurichthys zoster* is chiefly a diurnal planktivore that takes primarily copepods, but also feeds on benthic organisms, especially alcyonarians.

Chaetodon corallicola Snyder

Observations in the western Pacific have indicated that the Hawaiian *C. corallicola* is closely related to, if not conspecific with, the widespread Indo-Pacific *C. kleini*. In Kona, this species is relatively numerous at depths below 20 m along the edge of the outer drop-off. In daylight it generally swims in loosely associated pairs that pick free-swimming organisms from the water column within a meter or so of the reef. At night it remains close among the coral—alert, but apparently inactive.

All 11 specimens (89: 75-96 mm) collected for study during afternoons had full stomachs (including fresh material), as listed in Table 31. The only evidence of bottom feeding among this material is the caprellid amphipods and hydroids, both taken from the same individual.

CONCLUSION.—*Chaetodon corallicola* is primarily a diurnal planktivore that feeds largely on copepods.

Chaetodon miliaris Quoy and Gaimard

Gosline and Brock (1960) noted that *C. miliaris* is one of the commonest inshore fishes. Although it is numerous in shallow water around Oahu, Brock and Chamberlain (1968), using a submarine off that island, found it even more abundant in deeper water. They discovered it to be a dominant form at depths below 120 m, where it hovered in aggregations 15 to 40 m above the sea floor, apparently feeding on plankton. In the Kona study area, this species rarely occurs in water shallower than 20 m, but is numerous along the outer drop-off at 30 m and deeper. During the day it aggregates 2 to 3 m above the reef, where it picks organisms from the plankton. At night it is scattered among the rocks and ledges, alert but apparently inactive.

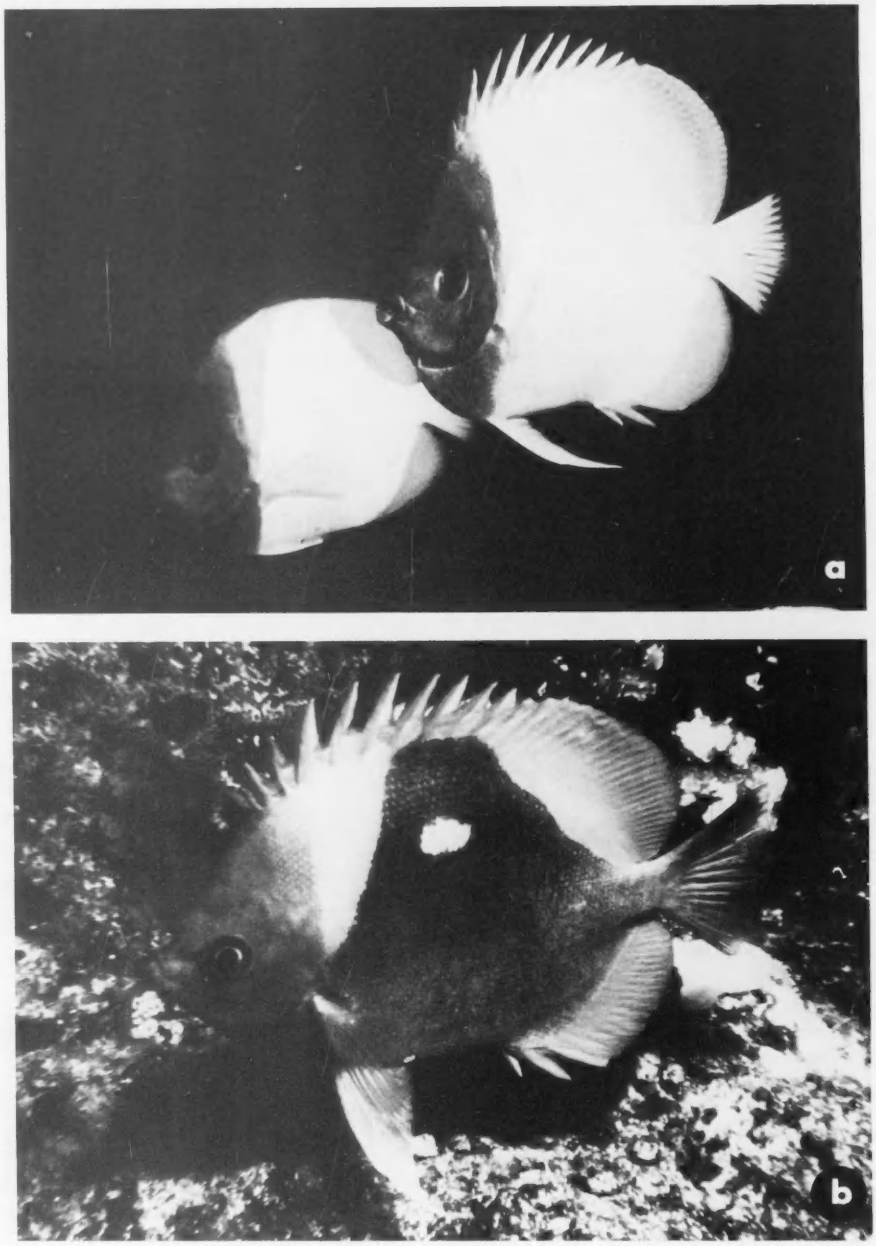

FIGURE 28.—*Hemitaurichthys zoster*, a butterflyfish: a, showing its diurnal coloration while swimming in the water column during the day; b, showing its nocturnal coloration while close to the reef at night.

TABLE 30.—Food of *Hemitaurichthys zoster*.

Rank	Items	No. fish with this item (n = 10)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	10	55.3	55.30
2	Alcyonarians	3	18.2	5.46
3	Cyclopoid copepods	8	6.1	4.88
4	Fish eggs, planktonic	6	1.9	1.14
5	Larvaceans	4	1.0	0.40
6	Blue-green algae in gelatinous sacs	3	1.3	0.39
7	Hydroids	2	1.9	0.38
8	Harpacticoid copepods	3	0.3	0.09
9	Gastropod veligers	2	0.3	0.06
10	Penaeid shrimps	1	0.2	0.02
11	Gastropod larvae, echinospira	1	0.1	0.01
12	Pelycypod larvae	1	0.1	0.01
13	Foraminiferans	1	<0.1	<0.01
14	Ostracods	1	<0.1	<0.01
Also, unidentified fragments		5	9.9	4.95
	Crustacean fragments	2	3.2	0.64

TABLE 31.—Food of *Chaetodon corallicola*.

Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	11	52.6	52.60
2	Cyclopoid copepods	11	12.1	12.10
3	Fish eggs, planktonic	9	1.3	1.06
4	Larvaceans	2	5.5	1.00
5	Ostracods	3	0.5	0.14
6	Lobster phyllosomes	3	0.5	0.14
7	Mysids	2	0.3	0.06
8	Caprellid amphipods	1	0.5	0.05
9	Salps	1	0.2	0.02
10	Shrimp larvae	1	0.2	0.02
11	Hydroids	1	0.1	<0.01
12	Gammaridean amphipods	1	<0.1	<0.01
13	Blue-green algae in gelatinous sacs	1	<0.1	<0.01
Also, unidentified fragments		11	26.0	26.00

Of eight specimens (118: 110-125 mm) collected, one that was taken during early morning twilight close among cover contained only a few well-digested fragments, whereas all seven that were active above the reef when taken during the afternoon were full of food (much of it fresh), as listed in Table 32.

CONCLUSION.—*Chaetodon miliaris* is a diurnal planktivore that takes mostly copepods.

Chaetodon quadrimaculatus Gray—four-spot butterflyfish

This butterflyfish is especially numerous where the water is less than 10 m deep over reefs rich in the coral *Pocillopora*. During the day it is active, solitary or paired, close to the sea floor. Feeding strictly on the bottom, it mostly picks at the surface of living coral or in cracks within dead coral and basalt. It occurs in the same areas at night, but though alert, seems relatively inactive.

Twenty-six specimens (92: 43-110 mm) were speared during day and night. All 15 collected during midday were full of food, as were 4 of 5 taken at night during the 2 h immediately before midnight (the fifth was empty). The remaining six were collected at night during the hour immediately before daybreak, and while three of these had empty stomachs, the other three were full. Whether these findings indicate nocturnal feeding or slow digestion remains uncertain. No differences were recognized in composition or condition of gut contents between specimens taken day and night. Items in the 22 individuals containing identifiable material are listed in Table 33.

At least some of the corals taken by this fish probably are soft corals. Most material in the gut appeared as amorphous clumps rich in nematocysts and zooxanthellae. That much of this is soft coral seems likely considering how often *C. quadrimaculatus* nibbles about reef crevices where living stony corals are absent.

TABLE 32.—Food of *Chaetodon miliaris*.

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	7	68.6	68.60
2	Cyclopoid copepods	7	2.8	2.80
3	Salps	1	3.0	0.43
4	Hyperiid amphipods	3	0.4	0.17
5	Fish eggs, planktonic	3	0.4	0.17
6	Larvaceans	1	0.9	0.13
7	Egg masses in gelatinous sacs	2	0.4	0.11
8	Ostracods	1	0.1	0.01
9	Harpacticoid copepods	1	0.1	0.01
10	Mysids	1	0.1	0.01
Also, unidentified fragments		6	23.2	19.89

TABLE 33.—Food of *Chaetodon quadrimaculatus*.

Rank	Items	No. fish with this item (n = 22)	Mean percent of diet volume	Ranking index
1	Anthozoans (no skeletal material)	22	81.4	81.40
2	Polychaetes (mostly tentacles and fragments)	13	6.2	3.66
3	Hydroids	13	1.6	0.95
4	Sipunculid introverts	7	1.9	0.60
5	Opisthobranch gastropods	3	1.3	0.18
6	Caprellid amphipods	6	0.4	0.11
7	Gammaridean amphipods	4	0.2	0.04
8	Cyclopoid copepods	2	0.1	<0.01
9	Calanoid copepods	1	<0.1	<0.01
10	Mites	1	<0.1	<0.01
11	Demersal eggs	1	<0.1	<0.01
Also, unidentified fragments		5	4.5	1.02
	Algal fragments, including diatoms	12	2.1	1.15

Opisthobranch gastropods had been taken by three of the individuals collected at night. Perhaps significantly, these same opisthobranchs are a major prey of *C. lunula* after dark (see below).

CONCLUSION.—*Chaetodon quadrimaculatus* feeds during the day mostly on corals, but also on polychaetes and other benthic organisms. Some nocturnal feeding is likely.

Chaetodon unimaculatus Bloch—one-spot butterflyfish

This chaetodontid is numerous on shallow reefs exposed to a strong surge where the coral *Pocillopora* is also abundant. Generally occurring in pairs, it is active during the day, picking at the surface of living *Pocillopora*, and to a lesser extent other reef surfaces. At night it is alert, but appears inactive as it hovers close among cover on the reef.

Twenty-six specimens (85: 66-102 mm) were speared during night and day. Of three that were collected during the 2 h immediately before midnight, two had empty stomachs, and the third contained a few well-digested fragments. Of four collected during the hour immediately before daybreak, two had empty stomachs, and two contained only well-digested fragments. Thus, there was no evidence of recent feeding by individuals taken after dark. In contrast, all 19 specimens collected during the day had full stomachs, including fresh material, as listed in Table 34.

The major food item, scleractinian corals (mostly *Pocillopora*), included many skeletal fragments.

CONCLUSION.—*Chaetodon unimaculatus* feeds during the day, mostly on the coral *Pocillopora*.

Chaetodon multicinctus Garrett—pebbled butterflyfish

Chaetodon multicinctus is probably the most numerous chaetodontid on Kona reefs in water

TABLE 34.—Food of *Chaetodon unimaculatus*.

Rank	Items	No. fish with this item (n = 19)	Mean percent of diet volume	Ranking index
1	Scleractinian corals	15	45.3	35.76
2	Sponges	5	12.4	3.26
3	Gammaridean amphipods	4	1.3	0.27
4	Pelycypods	1	3.2	0.17
5	Sipunculid introverts	1	1.6	0.08
6	Calanoid copepods	2	0.3	0.03
Also, unidentified fragments		18	29.1	27.57
	Algal fragments and diatoms	9	6.8	3.22

TABLE 35.—Food of *Chaetodon multicinctus*.

Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Scleractinian coral polyps	11	91.6	91.60
2	Gammaridean amphipods	7	1.8	1.15
3	Sipunculid introverts	5	1.3	0.59
4	Polychaetes (fragments and tentacles)	3	0.4	0.11
5	Hydroids	2	0.2	0.04
6	Calanoid copepods	1	0.1	0.01
Also, unidentified fragments		2	3.4	0.62
	Algal fragments and diatoms	6	1.2	0.66

shallower than 20 m, especially where stony corals abound. During the day it generally occurs in pairs, and is active close to the reef, often picking at living corals—both *Porites* and *Pocillopora*. At night it rests close among cover on the reef, alert but apparently inactive.

Of the 26 specimens (84: 78-94 mm) examined, all 15 that were collected at night (between 4 h after sunset and first morning light) were empty, whereas all 11 that were collected during midday were full of food (including fresh material), as listed in Table 35.

More so than the other butterflyfishes that feed on stony corals, *C. multicinctus* does so without also taking fragments of the surrounding skeleton.

CONCLUSION.—*Chaetodon multicinctus* is a diurnal predator that feeds primarily on scleractinian corals (mostly *Porites* and *Pocillopora*).

Chaetodon ornatissimus Solander—ornated butterflyfish

This butterflyfish is numerous over coral-rich reefs, generally swimming in pairs during the day. It moves from one growth of coral to another, locating and working its mouth over abrasions on the surface of the coral. In this way it feeds on a variety of scleractinian corals, including *Porites*, *Pavona*, and *Cyphastrea*. At night it rests quiet, but alert, close among cover on the reef. Its daytime and nighttime colorations differ strikingly (Figure 29a and b).

Nineteen specimens (119: 95-140 mm) were examined. All eight that were collected at night, later than 4 h after sunset and before first morning light, had the stomachs and anterior half of the intestines empty. All four that were taken during morning twilight—the earliest 25 min before sunrise—had material in their stomachs, but their intestines were empty (apparently they had just begun to feed). Finally, all seven that were collected during midday were full of food.

All 11 specimens with material in their stomachs contained only a thick mucus rich in nematocysts, zooxanthellae, and organic debris (mean percent of diet volume and ranking index: 99.8). The balance of the gut contents was made up of diatoms and a few algal fragments.

It is well known that stony corals increase their production of mucus when injured, so this chaetodontid's habit of seeking out abrasions on coral may explain why its gut contents include so much mucus. This species probably obtains significant nourishment from coral mucus, but judging from the numbers of zooxanthellae and

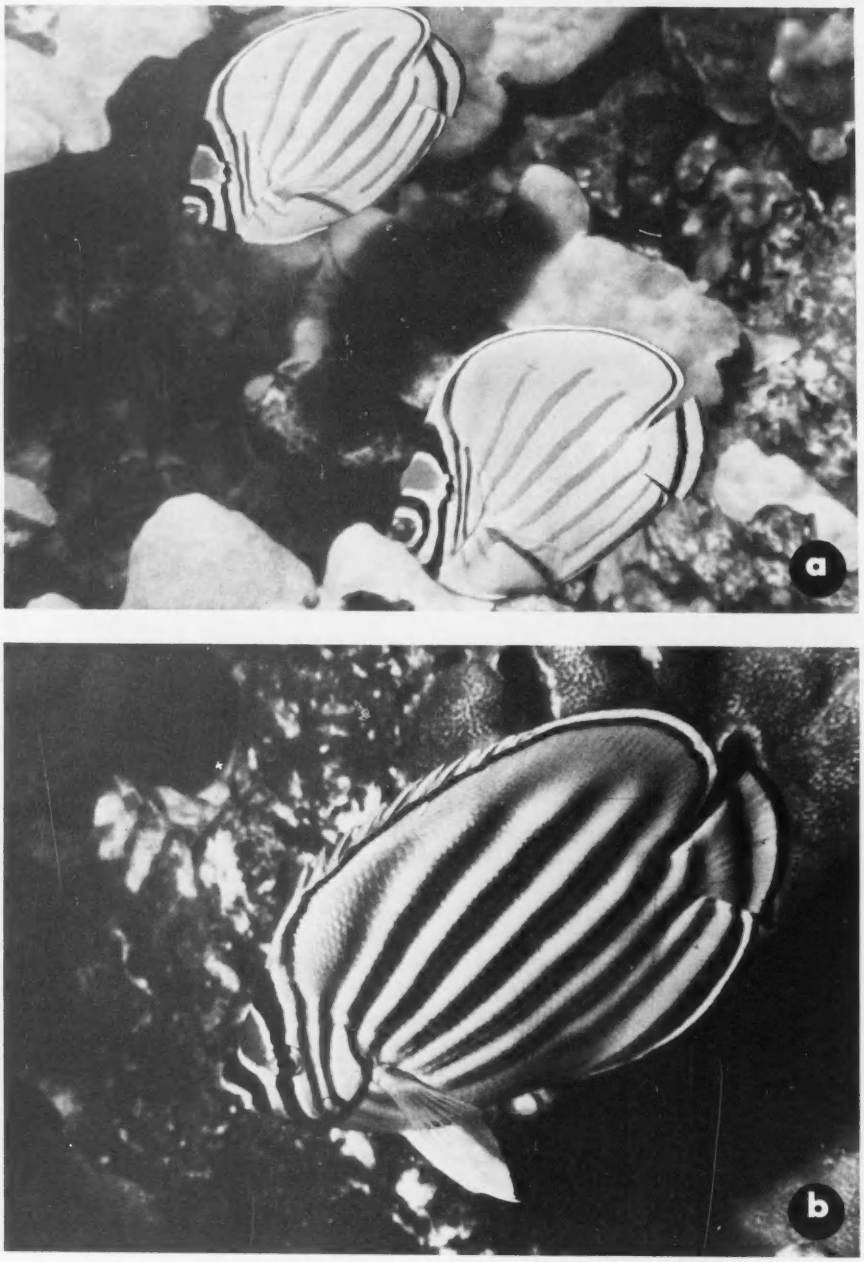

FIGURE 29.—*Chaetodon ornatissimus*, a butterflyfish: a, showing its diurnal coloration while swimming above the reef during the day; b, showing its nocturnal coloration while close to the reef at night.

nematocysts present, at least some coral tissue is also taken (although nothing was found recognizable as such). Presumably at least much of this material had been freshly ingested, because it came from individuals that were actively feeding when collected. Johannes (1967) and Coles and Strathman (in press) have shown there are significant quantities of organic material in coral mucus that could nourish a wide range of animals, including fishes. A similar butterflyfish, *Chaetodon trifasciatus,* not numerous in Kona, has feeding behavior similar to *C. ornatissimus.*

CONCLUSION.—*Chaetodon ornatissimus* is a diurnal fish that feeds on coral during the day, obtaining significant nourishment from coral mucus.

Chaetodon auriga Forskål

In Kona this chaetodontid is less abundant than many of its congeners. Generally paired, it swims close to the reef in daylight, occasionally picking at objects on the sea floor. At night it is alert close among ledges and other reef irregularities.

All six specimens (151: 132-160 mm) collected had full stomachs including four taken during the afternoon and two taken on a dark night, 3 h after sunset. All these specimens contained similar prey in what seemed similar condition. The data are too few to draw conclusions regarding nocturnal activity, but suggest that this species may feed after dark. Items in the stomachs of these six specimens are listed in Table 36.

Most of the food items were fragmented, including the unidentified material, and many of them were relatively fresh. Clearly, this chaetodontid obtains most of its food by tearing pieces from larger sessile organisms. Hiatt and Strasburg (1960) found similar prey in *C. auriga* from the Marshall Islands.

CONCLUSION.—*Chaetodon auriga* preys on a wide variety of benthic organisms during the day, obtaining most of its food by tearing off pieces of larger sessile animals. It also seems to feed to some extent after dark.

Chaetodon fremblii Bennett—blue-striped butterflyfish

This butterflyfish is most numerous where large basalt boulders are interspersed with small pockets of sand. Sometimes paired, but more often solitary, this chaetodonid picks at objects on the rocks and in the sand during the day. At night it occurs close among cover, alert but seemingly inactive.

Fourteen specimens (103: 86-120 mm) were speared during day and night. All eight collected during the afternoon had full stomachs, whereas the two taken from among rocks at night, between 4 and 5 h after sunset, were empty. On the other hand, three others collected together among the rocks during morning twilight, about 25 min before sunrise after a moonless night, had material in their stomachs. Two of them contained only a few well-digested fragments that could have been

TABLE 36.—Food of *Chaetodon auriga.*

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Alcyonarians	5	31.0	25.83
2	Terebellid polychaete tentacles	6	18.4	18.40
3	Gastropod egg masses	6	8.8	8.80
4	Errant polychaete fragments	5	5.4	4.50
5	Sabellid polychaete radioles	4	2.2	1.47
6	Echinoid podia	4	2.0	1.33
7	Caridean shrimps	4	1.4	0.93
8	Anemones	1	4.0	0.67
9	Sponges	1	3.1	0.52
10	Sipunculid introverts	3	0.4	0.20
11	Gammaridean amphipods	3	0.4	0.20
12	Hydroids	1	0.2	0.03
13	Serpulid polychaete fragments	1	0.2	0.03
Also, Unidentified fragments		6	20.7	20.70
	Algal fragments	3	1.8	0.90

taken the previous day, but in the third individual a wide variety of differentially digested items indicated either nocturnal feeding or unusually slow digestion. A fourth individual taken during morning twilight was empty. Items in the eight specimens containing identifiable material, much of it fragments torn from larger sessile animals, are listed in Table 37.

CONCLUSION.—*Chaetodon fremblii* preys on a wide variety of benthic organisms during the day, obtaining much of its food by tearing off pieces of larger sessile animals. With some uncertainty, it seems largely inactive after dark.

Chaetodon lunula (Lacépède)—masked butterflyfish

This butterflyfish, one of the more numerous in Kona, is most abundant where a coral-crested reef face falls among basalt boulders, yet occurs in a variety of habitats. Setting it apart from all other chaetodontids reported here, I never saw this species feed during the day. It generally hovers close to the reef in daylight, sometimes solitary, or in twos or threes, and often in large aggregations (Figure 30). These aggregations form day after day in the same locations, and several occurred in the same places over the entire 15-mo period of the study. The aggregations disperse at nightfall, and after dark the species scatters over the reef, either solitarily, or in twos or threes.

Of the 26 specimens (134: 112-150 mm) examined, all 14 speared at night (more than 4 h after sunset), or during morning twilight, had stomachs full of food in varying stages of digestion, much of it fresh; the other 12 were collected during afternoons (some from the daytime aggregations), and although they too had full stomachs, the contents generally were further digested. There was no recognizable difference in the composition of the diet between specimens collected during each of these three periods. Items in the stomachs are listed in Table 38.

Clearly, *C. lunula*, like *C. auriga* and *C. fremblii*, habitually tears pieces off the bodies of larger sessile animals, but, more so than the others, also takes whole organisms. In fact, its major prey, based on these data, are opisthobranch gastropods, which it takes whole. The opisthobranchs are mostly one form of Anaspidea and one form of Cephalaspidea. Significantly, all individuals of *C. lunula* that contained what seemed to be freshly ingested opisthobranchs were speared at night. Opisthobranchs in *C. lunula* speared during the afternoon were consistently far digested. These opisthobranchs are mostly about 4 to 10 mm long, and are relatively solid pieces of meat that may take longer to digest than many other kinds of food. Similarly, the polychaete heads and prosobranch gastropod heads taken by this fish are relatively dense pieces of meat that probably resist digestion (the shells of the prosobranch gastropods were never present—only the heads, which this butterflyfish apparently is adept at snipping off). Smaller organisms that would be rapidly digested like the amphipods and isopods, generally, but with two exceptions, were absent in specimens speared during the afternoon. Generally then, the stomach contents appeared to have been taken mostly at night. Finally, it may be significant that the eyes of *C. lunula* are relatively larger than the eyes of all other species of this genus studied at Kona.

TABLE 37.—Food of *Chaetodon fremblii*.

Rank	Items	No. fish with this item (n = 8)	Mean percent of diet volume	Ranking index
1	Terebellid polychaete tentacles	6	25.0	18.75
2	Sipunculid introverts	6	15.0	11.25
3	Gammaridean amphipods	8	10.1	10.10
4	Errant polychaete fragments	4	3.1	1.55
5	Hydroids	2	2.9	0.73
6	Isopods	3	1.6	0.60
7	Gastropod egg capsules	1	3.6	0.45
8	Caprellid amphipods	1	2.3	0.29
9	Acorn worms	1	2.3	0.29
10	Opisthobranch gastropods	1	1.4	0.18
11	Caridean shrimps	1	0.1	0.01
12	Gastropod opercula	1	0.1	0.01
Also, unidentified fragments		6	21.3	15.98
	Algal fragments	7	11.2	9.80

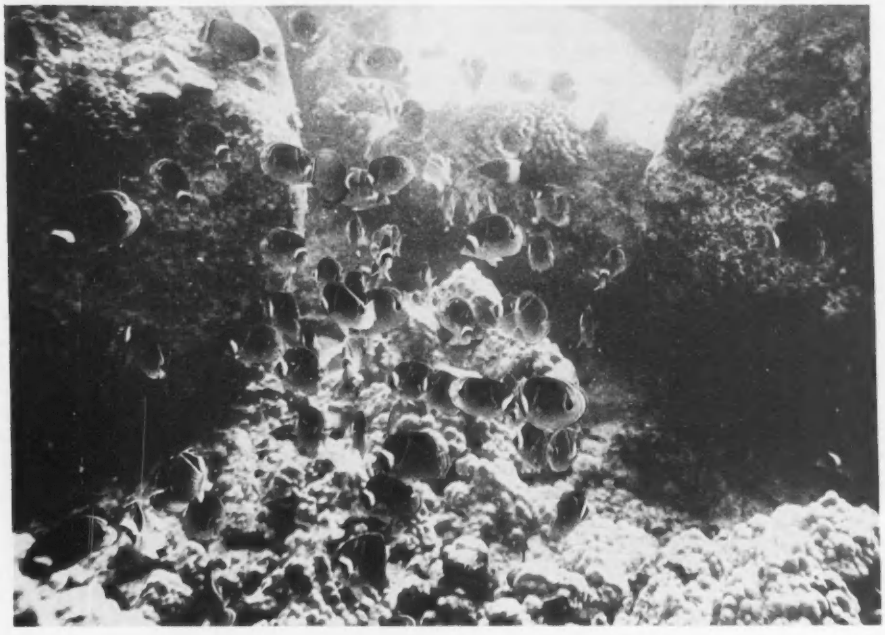

FIGURE 30.—Diurnal aggregation of *Chaetodon lunula*, a butterflyfish.

TABLE 38.—Food of *Chaetodon lunula*.

Rank	Items	No. fish with this item (n = 26)	Mean percent of diet volume	Ranking index
1	Opisthobranch gastropods	21	29.2	23.58
2	Terebellid polychaete tentacles	11	8.7	3.68
3	Errant polychaete fragments	17	2.2	1.44
4	Sipunculid introverts	9	1.7	0.59
5	Polychaete heads	8	1.9	0.58
6	Prosobranch gastropod heads	7	0.7	0.19
7	Gammaridean amphipods	9	0.3	0.10
8	Holothurians	2	1.3	0.10
9	Fish eggs	2	1.1	0.08
10	Caridean shrimps	4	0.3	0.05
11	Echinoid podia	4	0.2	0.03
12	Alcyonarians	2	0.3	0.02
13	Sabellid polychaete radioles	3	0.2	0.02
14	Caprellid amphipods	3	0.1	0.01
15	Crustacean eggs	1	0.2	<0.01
16	Tanaids	2	0.1	<0.01
17	Hydroids	2	0.1	<0.01
18	Anemones	1	0.1	<0.01
19	Calanoid copepods	1	0.1	<0.01
20	Crabs	1	0.1	<0.01
21	Tunicates	1	0.1	<0.01
Also, unidentified fragments		24	50.3	46.43
	Algal fragments	5	0.5	0.10
	Crustacean fragments	4	0.2	0.03

Hiatt and Strasburg (1960) noted only tips of coral polyps in one *C. lunula* from the Marshall Islands. Although the diet of this individual diverges sharply from that of representatives in Kona, one cannot speculate on its significance from one specimen.

CONCLUSION.—*Chaetodon lunula* preys on benthic invertebrates, especially opisthobranchs, at night.

General Remarks on Angelfishes and Butterflyfishes

The two Hawaiian angelfishes, *Holacanthus arcuatus* and *Centropyge potteri*, have feeding habits that set them apart from the butterflyfishes. *Holacanthus arcuatus* is the only chaetodontid that feeds strictly on sponges, and *C. potteri* is the only one that takes just algae and detritus. Thus the Hawaiian situation parallels that in the tropical Atlantic, where species of *Holacanthus* and of *Pomacanthus* (another genus of angelfish) feed mostly on sponges and where species of *Centropyge* feed almost exclusively on algae and detritus (Randall, 1967). Similarly, Hiatt and Strasburg (1960) reported a strictly herbivorous diet for *C. flavissimus* in the Marshall Islands.

Although butterflyfishes in Kona are more strictly predators in the conventional sense than are the angelfishes, Hiatt and Strasburg (1960) reported *Chaetodon reticulatus* in the Marshall Islands to be strictly herbivorous. That species is seen only occasionally in Kona, and so was not included in the present study. Otherwise, Hiatt and Strasburg found scleractinian corals and polychaetes to be the major food of butterflyfishes in the Marshall Islands, and this is in broad accord with the habits of certain species in Kona. Randall (1967) reported that West Indian butterflyfishes feed primarily on anthozoans and the tentacles of polychaetes, again paralleling the habits of certain Kona species. On the other hand, the number of planktivorous butterflyfishes in Kona seems on a scale without parallel in published accounts of other reef areas.

Chaetodontids have been widely described as diurnal fishes, e.g. in the tropical Atlantic (Starck and Davis, 1966; Collette and Talbot, 1972), and in the Gulf of California (Hobson, 1965, 1968a). Although diurnal habits are generally characteristic of chaetodontids in Kona, the fact that at least one, *Chaetodon lunula*, is nocturnal and that several others feed at least somewhat after dark may reflect increased interspecific pressures associated with the large number of *Chaetodon* species on Kona reefs. I treat the nine most numerous species of *Chaetodon* here, but also saw five others during this study.

Family Pomacentridae: damselfishes

Plectroglyphidodon johnstonianus Fowler and Ball

This solitary species is most numerous where stony corals abound. During the day it swims close to the reef, each individual seemingly associated with a particular location, and here it picks frequently at the substratum, especially around coral. At night it is secreted deep among the coral, relatively inactive, but alert.

Of the eight specimens (60: 39-70 mm) examined, the stomachs of two that were speared among the coral shortly before dawn contained only a few well-digested fragments (probably material that had been ingested during the previous day), whereas the stomachs of all six taken during midday were full of food, much of it fresh.

The major food item in all six was anthozoans: nematocysts and zooxanthellae, with tissue fragments and mucus, but no skeletal material (mean percent of diet volume and ranking index: 94.3). All other items made up only a minor part of the diet: algal fragments in three (mean percent of diet volume: 2; ranking index: 1), sipunculid introverts in one (mean percent of diet volume: 0.2; ranking index: 0.03), and unidentified fragments in four (mean percent of diet volume: 3.5; ranking index: 2.33). Because *P. johnstonianus* is closely associated with scleractinian corals, these probably are the anthozoans so prominent in its diet. However, specific identifications of the fragmented gut contents remain uncertain, and because direct observations of feeding are limited, other anthozoans may also be involved. In any event, the observations indicate that this fish is adept at snipping off pieces of anthozoan tissue and mucus without taking any of the surrounding skeletal material.

CONCLUSION.—*Plectroglyphidodon johnstonianus* is a diurnal predator that feeds chiefly on anthozoans.

Pomacentrus jenkinsi Jordan and Evermann

This species is one of the more widespread and numerous in Kona, especially in relatively quiet water over coral and rocks. During the day, individuals are scattered among reef irregularities, each seemingly associated with specific locations, and here they pick at coral and rock surfaces. At night they hover under cover, remaining alert but relatively inactive until shortly after first light, when diurnal activity is resumed.

Twenty-two specimens (89: 80-100 mm) were collected during day and night. All 12 that were speared as they swam close to the reef during midday were full of food, much of it fresh, whereas of 5 that were speared in reef crevices at night (between 4 and 5 h after last evening light), the stomachs of 3 were empty and those of the other 2 contained only a few well-digested, unidentified fragments. Finally, of five active individuals that were collected during morning twilight and during the first 30 min after sunrise, two were empty, and three contained in their stomachs a few fresh fragments that appeared to have been recently ingested. The 15 specimens that contained at least some fresh material had consumed the items listed in Table 39.

The amorphous organic fragments that constituted the bulk of the gut contents in this fish were in part items that had been digested beyond recognition; however, most of this material appeared to be detritus—organic deposits—that had been scraped from the reef. Gosline and Brock (1960) noted that *P. jenkinsi* inhabits quiet water, where it feeds on algae, and perhaps detritus. Hiatt and Strasburg (1960) also found this fish in quiet water in the Marshall Islands and reported it to be primarily a herbivore that feeds occasionally on small fishes.

CONCLUSION.—*Pomacentrus jenkinsi* is a diurnal omnivore that takes mostly organic detritus, algae, and small animals from reef surfaces.

Abudefduf sindonis (Jordan and Evermann)

This damselfish occurs where basalt boulders are swept by a strong surge. Activity is limited to daylight; at night it remains under cover among the rocks.

All five specimens (91: 81-102 mm) were speared during the day, and their guts were full of the material listed in Table 40, much of it fresh. The amorphous organic fragments, the major food item, probably are largely detritus from the reef, such as is also taken by *Pomacentrus jenkinsi*, discussed above. Where a strong surge sweeps the boulder habitat, *A. sindonis* replaces *P. jenkinsi* in depths shallower than about 3 m.

Gosline and Brock (1960) noted that *A. sindonis* seems restricted to surge areas among lava rocks and appears to be omnivorous.

CONCLUSION.—*Abudefduf sindonis* is a diurnal omnivore that takes mostly organic detritus, algae, and small animals from the substratum.

Abudefduf sordidus (Forskål)—*kupipi*

Although juveniles of *A. sordidus* are prominent in tide pools, the adults, which are the largest of the Hawaiian pomacentrids, seem to occur only where a precipitous basalt reef face confronts a prevailing swell. In this situation large individuals of this species are fairly numerous among rocky crevices and close to boulders at the base of the reef. Generally a solitary fish, *A. sordidus* is

TABLE 39.—Food of *Pomacentrus jenkinsi*.

Rank	Items	No. fish with this item (n = 15)	Mean percent of diet volume	Ranking index
1	Algae, including diatoms	15	24.1	24.10
2	Sponges	6	5.7	2.28
3	Calanoid copepods	1	4.6	0.31
4	Errant polychaetes	2	2.0	0.27
5	Fish eggs, demersal	2	1.0	0.13
6	Cyclopoid copepods	4	0.4	0.11
7	Gammaridean amphipods	2	0.2	0.03
8	Barnacle cirri	1	0.1	<0.01
9	Pelecypod mollusks	1	0.1	<0.01
Also, amorphous organic fragments		15	60.1	60.10
	Sand	4	1.7	0.45

TABLE 40.—Food of *Abudefduf sindonis*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Algae, including diatoms	5	39.4	39.40
2	Polychaetes	4	2.2	1.76
3	Gammaridean amphipods	4	2.2	1.76
4	Caridean shrimps	1	7.0	1.40
5	Cyclopoid copepods	4	1.0	0.80
6	Hydroids	1	1.0	0.20
7	Sipunculid introverts	1	0.2	0.04
8	Insects	1	0.2	0.04
Also, amorphous organic fragments		5	46.8	46.80

TABLE 41.—Food of *Abudefduf sordidus*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Algae, including diatoms	5	35.0	35.00
2	Crabs	4	20.0	16.00
3	Sponges	4	12.2	9.76
4	Prosobranch gastropods	4	9.2	7.36
5	Gammaridean amphipods	5	4.4	4.40
6	Prosobranch gastropod eggs	2	1.2	0.48
7	Tanaids	3	0.6	0.36
8	Hydroids	2	0.4	0.16
9	Bryozoans	2	0.4	0.16
10	Polychaetes	2	0.4	0.16
11	Pycnogonids	2	0.4	0.16
12	Insects	1	0.4	0.08
Also, unidentified fragments		5	15.4	15.40

active only during daylight, close to the substratum. After dark it is secreted under rocky cover, alert but relatively inactive.

All five specimens (147: 129-160 mm) were speared during midday, and their guts were full of the material listed in Table 41, much of it fresh. Gosline and Brock (1960) reported that the young of *A. sordidus* are very prominent tide-pool inhabitants and that the omnivorous adults apparently live just outside of the reef edge.

CONCLUSION.—*Abudefduf sordidus* is a diurnal omnivore that takes chiefly algae and small animals from the substratum.

Abudefduf imparipennis (Sauvage)

This pomacentrid is numerous on shallow, surge-swept reefs where exposed basalt is dotted by the coral *Pocillopora meandrina*. It is a solitary, bright-eyed little fish that is active in daylight, and does not swim away from the substratum. Appearing tense and alert, even when hovering motionless at the base of a coral head, its movements are short but rapid darts from one spot to another. At night it takes shelter deep within reef crevices.

All 15 specimens (42: 29-50 mm) were active on the reef during the day when collected, and all contained food, including fresh material, as listed in Table 42. Gosline and Brock (1960) noted that this fish seems to occur over all rocky areas in the surge zone, and that it appears to be entirely carnivorous, with the predominant food organism being a polychaete annelid.

CONCLUSION.—*Abudefduf imparipennis* is a diurnal predator that feeds mainly on small benthic crustaceans and polychaetes.

Abudefduf abdominalis (Quoy and Gaimard)—*maomao*

This damselfish is most numerous where basalt boulders lie at the base of a vertical reef face in water 5 to 10 m deep. During daylight it hovers in aggregations high in the water column close to the

TABLE 42.—Food of *Abudefduf imparipennis*.

Rank	Items	No. fish with this item (n = 15)	Mean percent of diet volume	Ranking index
1	Gammaridean amphipods	12	12.6	10.08
2	Polychaetes	7	17.6	8.21
3	Cyclopoid copepods	9	7.1	4.26
4	Sipunculid introverts	8	1.9	1.01
5	Fish eggs, demersal	3	3.1	0.62
6	Unidentified eggs, demersal	4	1.8	0.48
7	Opisthobranch gastropods	2	1.7	0.23
8	Diatoms	6	0.5	0.20
9	Algae fragments	2	0.8	0.11
10	Prosobranch gastropod eggs	1	0.8	0.05
11	Isopods	2	0.4	0.05
12	Sponge spicules	1	0.3	0.02
13	Caprellid amphipods	1	<0.1	<0.01
14	Harpacticoid copepods	1	<0.1	<0.01
15	Caridean shrimps	1	<0.1	<0.01
16	Mites	1	<0.1	<0.01
17	Insects	1	<0.1	<0.01
Also, unidentified fragments		15	50.9	50.90

TABLE 43.—Food of *Abudefduf abdominalis*.

Rank	Items	No. fish with this item (n = 10)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	10	54.0	54.00
2	Cyclopoid copepods	8	6.5	5.20
3	Fragments of algae	4	2.6	1.04
4	Fish eggs, planktonic	4	2.0	0.80
5	Polychaetes	4	1.9	0.76
6	Decapod shrimps	4	1.7	0.68
7	Larvaceans	1	4.0	0.40
8	Harpacticoid copepods	4	0.8	0.32
9	Gelatinous clumps of blue-green algae	2	1.3	0.26
10	Pelecypod larvae	2	0.2	0.04
11	Penaeid shrimp larvae	1	0.2	0.02
12	Gastropod veligers	1	0.1	0.01
13	Naupilius larvae	1	0.1	0.01
Also, unidentified fragments		9	24.6	22.14

reef, where it picks organisms from the plankton. Although members of an aggregation are close to one another, each feeds independently. The plankters are taken with what seems to be a visually directed action in which the fish suddenly thrusts both jaws forward, then immediately retracts them. Presumably the sudden expansion of the oral cavity sucks the prey in.

A given aggregation maintains station over a particular location although its position in the water column is influenced by several factors. Fish size is important, because the larger individuals tend to be farther above the reef than the smaller ones. Prevailing light is another factor; thus, when clouds pass in front of the sun, and light diminishes, individuals of all sizes descend closer to the reef. In addition, the appearance of a large predator, or some other disturbance, intermittently sends this fish diving to cover on the reef. However, after such an event it quickly returns to its feeding stations in the water column.

As light progressively fades late in the day, this species gradually descends to the reef so that by evening twilight it is sheltered among the coral (Hobson, 1972). On dark nights it remains under cover, relatively inactive but alert; however, under bright moonlight it swims in exposed positions close to the reef. Then, during morning twilight, it begins to ascend to its daytime feeding stations in the water column (Hobson, 1972).

Of 14 specimens (142: 105-162 mm) examined, the 4 that were speared as they hovered among the rocks on dark nights (between 4 and 6 h after sunset) contained only well-digested fragments, whereas all 10 that were speared from mid-water aggregations during afternoons had their stomach full of food (including much fresh material), as listed in Table 43.

CONCLUSION.—*Abudefduf abdominalis* is a diurnal planktivore that preys primarily on copepods.

Dascyllus albisella Gill

Where corals are abundant, this damselfish is numerous to depths of at least 35 m. During daylight, it aggregates in the water column and picks small organisms from the plankton, much as does *Abudefduf abdominalis*, described above, and its aggregations rise and fall in the water column in response to the same variables that influence that species. Also like *A. abdominalis*, *D. albisella* descends to the reef during evening twilight and spends the night close among the rocks—under cover on dark nights, and in exposed positions when there is moonlight.

Twelve specimens (79: 42-95 mm) were collected during day and night. The six that were speared shortly before first morning light as they hovered among the coral contained only a few well-digested fragments (five were taken after nights of bright moonlight, one after a dark night). On the other hand, the six that were collected from aggregations in the water column during afternoons had stomachs full of food, including much fresh material as listed in Table 44.

Gosline and Brock (1960) reported that *D. albisella* occurs in small schools around certain large coral heads and listed stomach contents as follows: shrimp and crab larvae, mysids, and calanoid copepods.

CONCLUSION.—*Dascyllus albisella* is a diurnal planktivore that takes primarily larvaceans and copepods.

Chromis vanderbilti (Fowler)

This, the smallest pomacentrid in Kona, is numerous where exposed basalt ledges are interspersed with coral. During the day it aggregates in the water column, but even under bright sunlight rarely moves more than 50 cm above the reef. On overcast days it generally remains sheltered, and shortly before sunset is the first planktivorous damselfish to descend to cover on the reef (Hobson, 1972). At night, it usually remains out of sight deep within reef crevices, and in the morning is the last pomacentrid to appear.

All 12 specimens (38: 17-46 mm) taken from feeding aggregations during midday had stomachs full of food, including fresh material, as listed in Table 45.

CONCLUSION.—*Chromis vanderbilti* is a diurnal planktivore that takes primarily copepods and larvaceans.

Chromis leucurus Gilbert

Gosline and Brock (1960) considered *C. leucurus* to include two distinct color phases: in one the body is very dark anteriorly and abruptly white posteriorly; in the other, the whole body, except black pectoral base and white caudal fin, is mostly plain orange-brown. Although I followed this judgment when making the fish counts, the probability that at least two species are represented, and that neither one may in fact be *C. leucurus*, is currently under study by John E. Randall, B. P. Bishop Museum, and Stanley Swerdloff, Government of American Samoa. In any event, the specimens collected for study of food

TABLE 44.—Food of *Dascyllus albisella*.

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Larvaceans	6	43.1	43.10
2	Calanoid copepods	6	11.2	11.20
3	Cyclopoid copepods	6	9.2	9.20
4	Gelatinous clumps of blue-green algae	4	7.2	4.80
5	Fragments of algae	4	1.5	1.00
6	Decapod shrimp larvae	2	2.2	0.73
7	Fish eggs, planktonic	2	1.1	0.37
8	Hydroid fragments	1	0.2	0.03
9	Pelecypod larvae	1	0.2	0.03
10	Gammaridean amphipods	1	0.2	0.03
11	Harpacticoid copepods	1	0.2	0.03
Also, unidentified fragments		5	23.7	19.75

TABLE 45.—Food of *Chromis vanderbilti*.

Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	11	30.5	27.96
2	Larvaceans	8	21.7	14.47
3	Cyclopoid copepods	12	8.8	8.80
4	Polychaetes	5	0.9	0.38
5	Fish eggs, planktonic	4	0.9	0.30
6	Decapod shrimps	2	1.7	0.28
7	Harpacticoid copepods	3	1.1	0.28
8	Siphonophores	1	1.7	0.14
9	Gelatinous clumps of blue-green algae	2	0.5	0.08
10	Ostracods	1	0.5	0.04
11	Hyperiid amphipods	1	0.1	0.01
Also, unidentified fragments		12	31.1	31.10

habits, below, all represent the orange-brown form.

Of the two, the orange-brown form is the more numerous in Kona, but both abound over coral-rich reefs, often together in plankton-feeding aggregations that hover within 1 m of the substratum during the day. As is true of *Abudefduf abdominalis* and *Dascyllus albisella*, described above, *C. leucurus* remains closer to the reef when light is diminished, and dives to cover when threatened (Figure 31). At night it generally is out of sight within crevices.

All five specimens (57: 37-70 mm) speared during midday had their stomachs full of food, including fresh material, as listed in Table 46.

Swerdloff (1970a) described the behavior of two spatially related species of *Chromis* in the Marshall Islands, *C. leucurus*, and *C. dimidiatus*, and reported their food to be calanoid copepods, fish eggs, and larval tunicates.

CONCLUSION.—*Chromis leucurus* is a diurnal planktivore that takes primarily copepods and larvaceans.

FIGURE 31.—Members of an aggregation of *Chromis leucurus*, a damselfish, having been threatened, dive from their plankton-feeding location in the water column toward shelter among the coral below.

TABLE 46.—Food of *Chromis leucurus*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Cyclopoid copepods	5	19.0	19.00
2	Larvaceans	3	22.0	13.20
3	Calanoid copepods	3	4.0	2.40
4	Fish eggs, planktonic	4	2.8	2.24
5	Gelatinous clumps of blue-green algae	3	3.6	2.16
6	Fragments of algae	2	2.0	0.80
7	Harpacticoid copepods	1	0.4	0.08
Also, unidentified fragments		5	46.2	46.20

TABLE 47.—Food of *Chromis verater*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	5	29.6	29.60
2	Larvaceans	4	36.0	28.80
3	Cyclopoid copepods	5	2.2	2.20
4	Fish eggs, planktonic	3	2.4	1.44
5	Decapod shrimps	1	7.0	1.40
6	Siphonophores	1	0.8	0.16
7	Mysids	1	0.4	0.08
8	Chaetognaths	1	0.4	0.08
9	Polychaetes	1	0.2	0.04
10	Harpacticoid copepods	1	0.2	0.04
Also, unidentified fragments		5	20.8	20.80

Chromis verater Jordan and Metz

This damselfish is one of the more prominent fishes over both coral and basalt reefs in Kona at depths below about 15 m. During the day it swims in plankton-feeding aggregations that hover 2 to 5 m above the reef, where changing light levels and the appearance of certain predators produce effects much as described above for *Abudefduf abdominalis* and other planktivorous pomacentrids. Also as in these other species, *C. verater* passes the night among cover on the reef, relatively quiet but alert. It moves about under moonlight, but rests in crevices on dark nights.

Of the seven specimens (120: 100-141 mm) examined, two that were collected from among cover on the reef shortly before first morning light (one after a night of bright moonlight, the other after a dark night) contained only a few well-digested fragments, whereas, all five speared from aggregations above the reef during afternoons were full of food (including fresh material), as listed in Table 47.

Swerdloff (1970b), who recognized that *C. verater* inhabits relatively deep water, reported the following categories of prey in 13 specimens from one collection on the island of Oahu (ranked as percent of the diet): copepods, 71.5%; tunicates, 17.6%; malacostracans, 4.7%; mollusks, 2.5%; fish eggs, 1.7%; and siphonophores, 1.7%. He also presented additional data of food habits, as he compared the ecology of *C. verater* with that of its congener *C. ovalis* see below).

Gosline and Brock (1960) noted that *C. verater* occurs in deeper water than other Hawaiian pomacentrids. This conclusion was later supported by Brock and Chamberlain (1968) who, making observations from a submarine, found *C. verater* to be the most abundant reef fish around rocky outcrops at a depth of 70 m.

CONCLUSION.—*Chromis verater* is a diurnal planktivore that takes primarily copepods and larvaceans.

Chromis ovalis (Steindachner)

This species is less numerous in Kona than any of the other planktivorous damselfishes described above. It occurs over irregular substrata of exposed basalt interspersed with coral at depths between 5 and 20 m. During the day it aggregates 2 to 5 m above the reef—at about the same level as *C. verater*, with which it often forms mixed groups (Swerdloff, 1970b). Its reactions to changing light and threatening situations are as described above

TABLE 48.—Food of *Chromis ovalis*.

Rank	Items	No. fish with this item (n = 2)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	2	47.5	47.50
2	Larvaceans	2	7.5	7.50
3	Cyclopoid copepods	2	3.0	3.00
4	Mysids	1	2.5	1.25
5	Decapod shrimps	1	2.5	1.25
Also, unidentified fragments		2	37.0	37.00

for *Abudefduf abdominalis* and for other planktivorous pomacentrids; its nocturnal behavior also is like that described for these other species.

Of six specimens (124: 121-138 mm) examined, all four that were speared among corals shortly before first morning light (two after dark nights, two after moonlit nights) contained only a few well-digested fragments, whereas two that were speared from aggregations above the reef during midafternoon were full of food (including fresh items), as listed in Table 48.

Swerdloff (1970b) reported the following categories of prey in eight *C. ovalis* from one collection on the island of Oahu (ranked as percent of the diet): copepods, 60.1%; tunicates, 16.9%; malacostracans, 9.5%; mollusks, 9.5%; polychaetes, 2.3%; fish eggs, 0.8%; and siphonophores, 0.8%. Gosline and Brock (1960) reported "a mass of copepods" in the stomach of one individual of this species.

CONCLUSION.—*Chromis ovalis* is a diurnal planktivore that takes primarily copepods.

General Remarks on Damselfishes

Pomacentrids are widely recognized as being active by day and relatively inactive at night. For example, they were so described in the Gulf of California (Hobson, 1965, 1968a), and also in the tropical Atlantic (Starck and Davis, 1966; Collette and Talbot, 1972). Food-habit data from the various members of this family in areas as widely separated as the West Indies (Randall, 1967) and the Marshall Islands (Hiatt and Strasburg, 1960) show widely divergent habits: some are strictly herbivorous, others are omnivorous, and still others are strictly carnivorous.

The habitat of each pomacentrid in Kona is especially well defined. Two major categories exist: those that forage on the bottom and those that feed in the water column.

BOTTOM FEEDERS.—Pomacentrids that forage on the sea floor have especially diverse diets. Algae and organic detritus are the major foods of many, especially among species of *Pomacentrus* (Hiatt and Strasburg, 1960; Randall, 1967). In Kona, *P. jenkinsi* is in this category, but *P. pavo* in the Marshall Islands is primarily a predator on small fishes and crustaceans (Hiatt and Strasburg, 1960). The diets of species of *Abudefduf* appear even more diverse. *Abudefduf sindonis* in Kona has food habits similar to those of *P. jenkinsi*, but the highly omnivorous *A. sordidus* forages on a wide variety of benthic animals and plants, whereas the predaceous *A. imparipennis* takes mostly benthic crustaceans and polychaetes. *Abudefduf saxatilus* in the West Indies is, according to Randall (1967), "one of the most diversified of all fishes in its food habits," feeding as it does on a wide assortment of plants and animals from both sea floor and water column. Similarly, *A. troschelii* in the Gulf of California feeds on zooplankton and bits of algae from the water column, as well as organisms from the substratum (Hobson, 1968a).

WATER-COLUMN FEEDERS.—Planktivorous pomacentrids are prominent on coral reefs throughout tropical seas. Their characteristic mid-water aggregations have been described in the Indian Ocean (Eibl-Eibesfeldt, 1962), central Pacific (Hiatt and Strasburg, 1960), Gulf of California (Hobson, 1965, 1968a), and the tropical Atlantic (Starck and Davis, 1966). In the Bahamas, Stevenson (1972) showed that the height in the water column at which *Eupomacentrus partitus* feeds on plankton is determined largely by light and current. The progressive ascent of planktivorous pomacentrids into the water column during morning twilight, as they rise to their mid-water feeding grounds, and their subsequent descent to the reef during evening twilight, has been described in Kona (Hobson,

1972) and the West Indies (Collette and Talbot, 1972).

Some of these planktivorous pomacentrids, for example *Abudefduf saxatilus* and *A. troschelii*, noted above, also forage part time on the sea floor. However, most of them, including the species of *Chromis* and *Dascyllus*, are specialized as predators on zooplankton, especially copepods. Examples include the representatives of these genera on Kona reefs, described in the present report, as well as others from the central Pacific (Hiatt and Strasburg, 1960) and tropical Atlantic (Randall, 1967).

Family Cirrhitidae: hawkfishes

Paracirrhites arcatus (Cuvier)—*pili ko'a*

This hawkfish is numerous in areas richly overgrown by the coral *Pocillopora meandrina*. Typically, it rests immobile on the coral heads during day, and takes shelter among the coral branches at night. Individuals shorter than about 50 mm are among the coral branches day and night, whereas those longer than about 90 mm frequently occur on the other hard substrata—perhaps because they are too large to fit between the branches of most *Pocillopora* heads. *Paracirrhites arcatus* moves only infrequently—a short dash to capture prey, or when threatened.

Forty-five specimens (82: 49-101 mm) were collected during day and night. The nighttime situation is reflected in the 17 that were speared during the 2 h before first morning light (13 on moonlit nights, 4 on dark nights). Of these, 16 (52 to 95 mm) were resting among branches of *Pocillopora*, whereas the other (99 mm) was amid a fingerlike growth of *Porites compressus*. The stomachs were empty in 13 and contained only well-digested fragments in 3. The last individual, taken during new moon, contained a caridean shrimp that probably had been captured that night.

The daytime situation is reflected in the 12 individuals speared during afternoons, all perched in exposed positions on the reef when collected. Ten of these (71 to 101 mm) rested on *Pocillopora*, and two (95 and 97 mm) rested on rocks. Ten had stomachs full of food, much of it fresh, and although the remaining two had empty stomachs, their intestines were full.

Specimens collected at other times of day and night offer less conclusive data. Of nine speared at night (between 3 and 5 h after sunset), seven were deep among coral branches, but two rested in exposed positions (the latter situation was only rarely seen). Six of these had food in their stomachs, but although the material was well-digested in five, the sixth was full of a species of cyclopoid copepod that often swarmed around our diving lights for about 30 min, an hour or so after last evening light. Finally, of the seven speared within 2 h after sunrise as they rested on top of *Pocillopora* heads, four had the stomachs empty and three contained fresh prey. Identifiable material occurred in 20 of the 46 specimens examined, as listed in Table 49.

Hiatt and Strasburg (1960), reporting on this species from the Marshall Islands, remarked that it habitually lies motionless on the upper surface of living coral heads and listed a diet of crustaceans and fishes.

CONCLUSION.—*Paracirrhites arcatus* is a diurnal predator that feeds primarily on xanthid crabs and other benthic crustaceans.

Paracirrhites forsteri (Bloch and Schneider)—*hilu pili ko'a*

This hawkfish is numerous in coral-rich areas, where it rests immobile in exposed positions on the reef during the day (Figure 32). Its attitude is

TABLE 49.—Food of *Paracirrhites arcatus*.

Rank	Items	No. fish with this item (n = 20)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	12	43.3	25.98
2	Decapod shrimps	6	15.5	4.65
3	Fish	3	10.5	1.58
4	Ophiuroids	1	5.0	0.25
5	Calapid crabs	1	4.3	0.22
6	Cyclopoid copepods	1	4.0	0.20
7	Crab megalops	2	1.8	0.18
8	Gammaridean amphipods	2	0.5	0.05
9	Calanoid copepods	1	0.3	0.02
Also, crustacean fragments		6	13.5	4.05
	Unidentified fragments	1	1.3	0.07

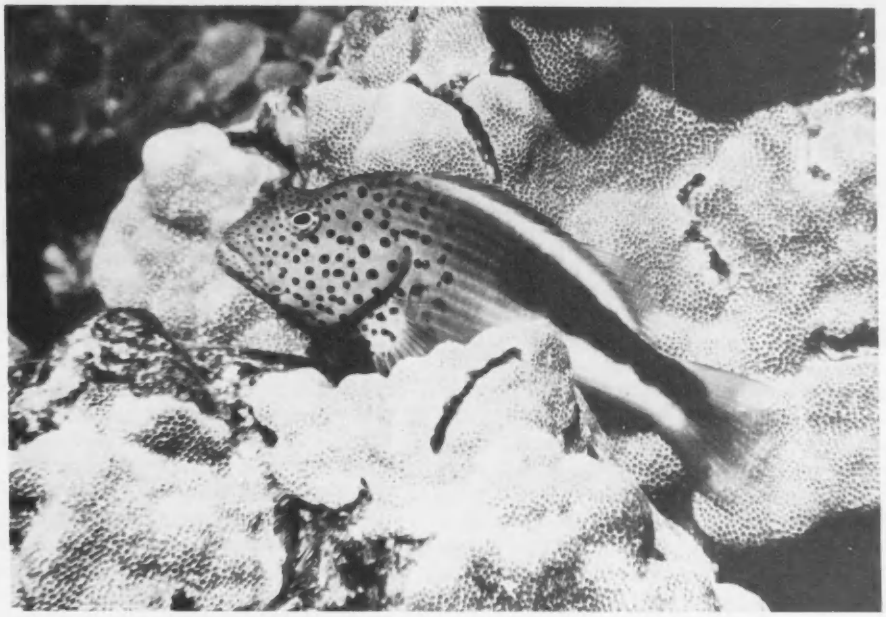

FIGURE 32.—*Paracirrhites forsteri*, a hawkfish, seated on the reef during the day.

much like that of *P. arcatus*, above, but it occurs widely on different hard surfaces, rather than being mostly associated, as is *P. arcatus*, with one type of coral. In the manner typical of hawkfishes, *P. forsteri* moves only infrequently, attacking prey that have come within range of a short, explosive dash. Such attacks were seen only during the day; at night *P. forsteri* generally is out of sight in reef crevices.

Thirty-six specimens (139: 93-181 mm) were collected during day and night. Of the 28 that were speared as they rested during midday on a variety of reef substrata, 18 contained food in the stomach, much of it relatively fresh (although in 1 the material was reduced to unidentifiable fragments). In contrast, among eight others that were speared from deep within reef crevices during the 2 h immediately before first morning light, four had empty stomachs and three contained only well-digested fragments; only the eighth specimen contained relatively fresh prey—a shrimp, *Saron marmoratus*—that appeared to have been taken that night.

Fish were the major prey, occurring in 14 of the 21 individuals that contained identifiable material (mean percent of diet volume: 66.6; ranking index: 44.4). Other food items were: caridean shrimps in four (mean percent of diet volume: 16.2; ranking index: 3.09), xanthid crabs in one (mean percent of diet volume: 4.8; ranking index: 0.23), and unidentified crustacean fragments in three (mean percent of diet volume: 12.4; ranking index: 1.77). The only identifiable fish among the gut contents was a wrasse, *Thalassoma duperrey*. Three of the four individuals containing caridean shrimps had preyed on *Saron marmoratus*. Of the larger shrimps (to about 50 mm), this was the one most frequently seen after dark, but only one of these, noted above, appeared to have been captured at night. Perhaps significantly, the specimens of *P. forsteri* that were examined had preyed on either fishes or crustaceans, but never on both.

Hiatt and Strasburg (1960), citing the similarity in habits between *P. forsteri* and *P. arcatus*, noted that the diet of *P. forsteri* runs more to fishes than crustaceans. I agree with them that this difference probably relates to the size difference between these two congeners.

CONCLUSION.—*Paracirrhites forsteri* is a diurnal predator that preys mostly on small fishes.

Cirrhitops fasciatus (Bennett) — *'o'opu kaha 'iha 'i*

This hawkfish is numerous on both coral and basalt reefs, and unlike the two species of *Paracirrhites,* above, occurs in exposed positions at night as well as during the day. In typical hawkfish fashion, it generally rests immobile on the substratum, except when attacking prey; thus, it is difficult to differentiate periods of activity from periods of inactivity.

Twenty-three specimens (76: 39-91 mm) were collected during night and day. Seven of nine speared from exposed positions under moonlight between 4 and 5 h after sunset contained prey that appeared to have been recently ingested. In addition, three of six individuals taken during the hour immediately before first morning light also contained relatively fresh prey. The daytime situation is reflected by specimens that were collected during afternoons, where the stomachs from six of eight individuals contained prey, much of it relatively fresh. Items in the 16 specimens containing identifiable prey are listed in Table 50.

CONCLUSION.—*Cirrhitops fasciatus* regularly feeds during both day and night, mostly on xanthid crabs and other benthic crustaceans.

Cirrhitus pinnulatus (Bloch and Schneider)— *po'o pa'a*

This hawkfish is numerous at depths of less than 5 m in and around crevices on surge-swept basalt reefs (Figure 5). Corals in this habitat are mostly isolated heads of *Pocillopora meandrina* and encrusting patches of *Porites compressus.* As do other hawkfishes, *C. pinnulatus* generally rests motionless on the substratum. During the day it usually remains under at least partial cover; at night it more frequently occurs in exposed positions on the reef.

All 32 specimens (152: 103-221 mm) that were examined were resting immobile on the reef when speared, most of them partially concealed in crevices. Of 17 taken during the afternoon, 14 had empty stomachs, and 3 contained material extensively damaged by digestion. In contrast, of 15 that were taken between 1 h before first morning light and 2 h after sunrise, only 4 had empty stomachs, whereas each of the other 11 had the stomach full of food, much of it fresh. Items in the 14 individuals containing identifiable material are listed in Table 51.

Most of the xanthid crabs among these gut contents were *Trapezia,* a genus common among branches of the coral *Pocillopora.* Hiatt and Strasburg (1960) also reported a crab of this genus in one *C. pinnulatus* that they examined from the

TABLE 50.—Food of *Cirrhitops fasciatus.*

Rank	Items	No. fish with this item (n = 16)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	7	30.9	13.52
2	Decapod shrimps	5	20.9	6.53
3	Crab megalops	2	7.8	0.98
4	Ophiuroids	1	6.3	0.39
5	Octopods	1	6.3	0.39
6	Gammaridean amphipods	1	0.6	0.04
Also, crustacean fragments		5	22.2	6.94
	Unidentified fragments	1	5.0	0.31

TABLE 51.—Food of *Cirrhitus pinnulatus.*

Rank	Items	No. fish with this item (n = 14)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	11	60.0	47.14
2	Oxyrhynchan crabs	3	7.5	1.61
3	Decapod shrimps	3	2.9	0.62
4	Ophiuroids	1	7.1	0.51
5	Octopods	1	7.1	0.51
6	Echinoids	1	3.2	0.23
7	Pagurid crabs	1	1.1	0.08
Also, crustacean fragments		3	11.1	2.38

Marshall Islands. Randall (1955) reported only brachyuran crabs in the diet of two specimens that he examined from the Gilbert Islands.

CONCLUSION.—*Cirrhitus pinnulatus* is a nocturnal predator that hunts mostly xanthid crabs.

Family Labridae: wrasses

Bodianus bilunulatus* (Lacépède) — *'a'awa

This relatively large, solitary wrasse occurs only infrequently on the shallow reefs in Kona as it lives mostly at depths below 15 m. Two individuals (172 and 283 mm) were speared during midafternoon as they moved actively among coral at 25 m along the outer drop-off, and the guts of both were full of crushed mollusks.

CONCLUSION.—*Bodianus bilunulatus* feeds on mollusks during the day.

Cheilinus rhodochrous* Günther—*po'ou

This labrid is numerous over both coral and rocky substrata deeper than about 10 m. It is a solitary species that hovers close to the reef during the day and takes shelter in the reef at night. Several times larger individuals attempted to take fish that were impaled on my spear, and twice they succeeded despite my attempts to drive them away.

Among 16 specimens (175: 129-242 mm) collected during afternoons, 6 contained only a few well-digested fragments posteriorly in the gut, and most of the material in the other 10 was far digested. Fish were the major prey, occurring in 4 of the 10 individuals that contained identifiable material (mean percent of diet volume: 40; ranking index: 16). Other food items were: decapod shrimps in three (mean percent of diet volume: 30; ranking index: 9), brachyuran crabs in one (mean percent of diet volume: 8; ranking index: 0.8), unidentified crustacean fragments in two (mean percent of diet volume: 12; ranking index: 2.4), and other unidentified fragments in two (mean percent of diet volume: 10; ranking index: 2). The only fish that could be identified was a pomacentrid, *Pomacentrus jenkinsi*, and the only identifiable shrimp was *Saron marmoratus*. Generally *C. rhodochrous* preys on large organisms, but because it crushes them upon ingestion, identifications are difficult. Presumably crushing the food items accelerates digestion, thus contributing to the poor condition of this material. However, because all these specimens were collected during afternoons, the advanced digestion could also reflect early morning feeding.

Cheilinus rhodochrous is a stalking predator, equipped by a relatively large mouth and pair of large canine teeth at the front of each jaw to hunt prey that are relatively larger and more active than those taken by most other labrids. Most of the specimens that were examined contained a single large prey organism, indicating that feeding is infrequent and that each successful attack provides enough nourishment to sustain the predator for some time.

CONCLUSION.—*Cheilinus rhodochrous* is a diurnal predator that stalks relatively large fishes and crustaceans. It may have peaks in feeding early and late in the day, but is inactive at night.

***Pseudocheilinus octotaenia* Jenkins**

This small species is one of the more numerous labrids on coral-rich reefs at depths to at least 30 m, but its large numbers are difficult to appreciate because it occurs close among the many narrow interstices of the reef. It is strictly a diurnal species that takes shelter in the reef at night.

All 12 specimens (77: 50-95 mm) taken during afternoons had material in their stomachs, but the food items were difficult to identify because they were small and had been crushed when ingested. Thus, most of the gut contents of all 10 individuals that contained recognizable material can be listed only as unidentified crustacean fragments (mean percent of diet volume and ranking index: 71.9). Items that could be identified are: brachyuran crabs in three (mean percent of diet volume: 22; ranking index: 6.6), echinoids in one (mean percent of diet volume: 5; ranking index: 0.5), demersal fish eggs in one (mean percent of diet volume: 1; ranking index: 0.1), and copepods in one (mean percent of diet volume: 0.1; ranking index: 0.01).

CONCLUSION.—*Pseudocheilinus octotaenia* is a diurnal predator that feeds mostly on brachyuran crabs and other benthic crustaceans.

***Labroides phthirophagus* Randall**

This small wrasse (most are less than 100 mm long) is specialized to pick ectoparasites from the

bodies of other fishes at well-defined cleaning stations (Figure 33). Usually two or several of these cleaners are active at each station. It is a diurnal species that shelters in reef crevices at night (Hobson, 1972).

This is the major cleaner fish on Hawaiian reefs, and its habits are well known (e.g. Randall, 1958; Youngbluth, 1968; Losey, 1971; Hobson, 1971). Because the activity of this species has been extensively documented, it was only incidentally observed during the present study.

CONCLUSION.—*Labroides phthirophagus* cleans ectoparasites from the bodies of other fishes during the day.

Thalassoma duperrey (Quoy and Gaimard) — *hinalea lauwili*

This is probably the most ubiquitous fish on Kona reefs (Figure 33): it is numerous everywhere, from the surge-swept reef tops to the outer drop-off on both coral-rich and exposed basalt substrata. In the daytime fish counts along transect lines, *T. duperrey* ranked among the five most numerous species in all the sampled habitats. An opportunist, it is consistently the first fish to appear when a sea urchin has been crushed, or when a rock has been overturned and vulnerable organisms exposed. Sometimes it follows close to the feeding jaws of scarids to snap up prey uncovered when these herbivores disturb the substratum. This wrasse is adapted to a wide range of habits: it forages in the water column when plankton are abundant, but mostly picks organisms off a variety of substrata. It is strictly a diurnal species that shelters in reef crevices at night (Hobson, 1972).

Many of the juveniles are cleaners and maintain stations at certain prominent coral heads. On one survey 5 m deep along approximately 1 km of the north shore of Honaunau Bay, I found a cleaning station maintained by these fish at every large head of *Porites pukoensis* that was of a distinctive mustardlike hue and characterized by golf-ball-sized nodules separated by narrow, shallow depressions. The general extent of this cleaner's relationship to this type of coral was not determined, but I saw cleaning stations nowhere else during the survey. Because the juveniles of *T. duperrey* always discontinued cleaning when a human was near, incidental observations of this activity were rare. And, as noted above in discussing *Labroides*

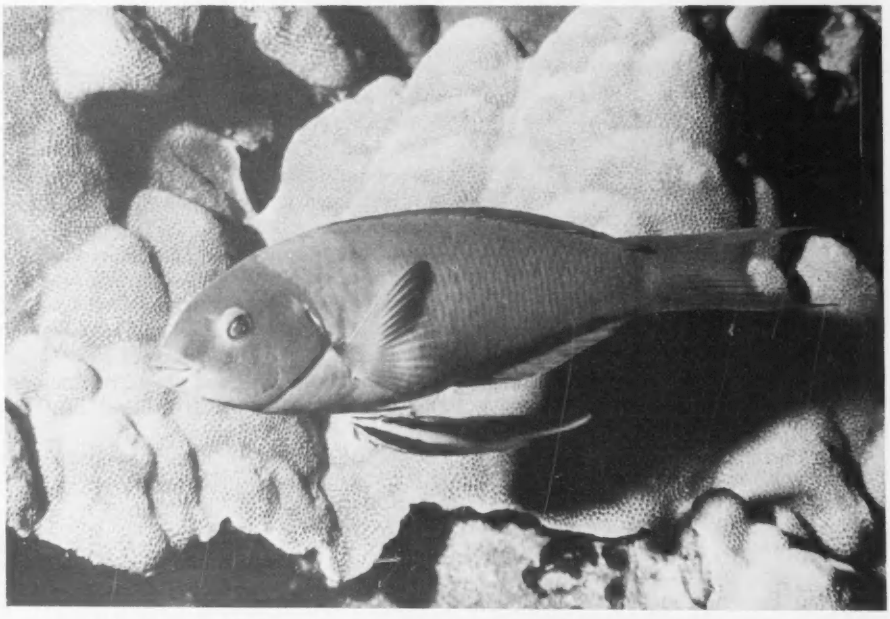

FIGURE 33.—A wrasse, *Thalassoma duperrey*, being cleaned by another wrasse, *Labroides phthirophagus*.

phthirophagus, my observations of cleaning were mostly incidental. Nevertheless, it was evident that cleaning by *T. duperrey* is mostly an activity of juveniles. Adults clean only infrequently, and not at well-defined cleaning stations.

To indicate the food of the post juveniles of this species, 24 specimens, 125 (103-146) mm long, were speared during the day as they swam actively over the reef. All contained identifiable items, as listed in Table 52. In contrast with the diet of most fishes examined during this study, no single item or certain few items predominate in the diet of *T. duperrey*, a circumstance that undoubtedly relates to its populating a wide range of habitats.

CONCLUSION.—*Thalassoma duperrey* is a diurnal predator that feeds on a very wide range of shelled organisms, most of them benthic.

Thalassoma fuscus (Lacépède)—*hou*

This species was shown by numerous observations of spawning aggregations to include the nominal *T. umbrostigma* (which represents the juveniles and females). It is a fish of shallow water along rocky, surge-swept shores and is one of the most numerous species on the shallow reef flats. Generally it does not occur in water deeper than about 5 m and is strictly a diurnal fish that shelters in reef crevices after dark.

All 14 specimens (132: 60-200 mm) speared as they swam on the reef during daylight contained identifiable food material, as listed in Table 53. Hiatt and Strasburg (1960) reported on two specimens of this species (as *T. umbrostigma)* in the Marshall Islands: one had consumed a stomatopod, the other a fish. Randall (1955) reported (also as *T. umbrostigma*) that one specimen taken in the Gilbert Islands contained a crab.

CONCLUSION.—*Thalassoma fuscus* is a diurnal predator that feeds mostly on crabs and mollusks.

Halichoeres ornatissimus (Garrett)—*la'o*

In Kona this labrid is nowhere particularly numerous, yet it occurs regularly in all inshore habitats. It is generally solitary and swims close to cover during the day. At night it is out of sight, presumably resting in crevices or under the sand.

All 13 specimens (96: 76-115 mm), speared during daylight, had a full gut that included fresh material, as listed in Table 54. Food items more than about 4 mm in greatest dimension were crushed, and this included most of the mollusks. Probably at least much of the unidentified material constituted fragmented molluscan soft parts. This fish plucks small benthic organisms off the substratum, including some forms, like the didemnid tunicates, that are attached to the reef.

TABLE 52.—Food of *Thalassoma duperrey*.

Rank	Items	No. fish with this item (n = 24)	Mean percent of diet volume	Ranking index
1	Gastropod mollusks	9	7.5	2.81
2	Echinoids	3	7.9	0.99
3	Brachyuran crabs	3	6.1	0.76
4	Pelecypod mollusks	3	5.0	0.63
5	Gammaridean amphipods	9	1.5	0.56
6	Calanoid copepods	2	6.3	0.53
7	Tanaids	6	1.3	0.33
8	Cyclopoid copepods	4	1.4	0.23
9	Scleractinian corals	2	2.5	0.21
10	Polychaetes	2	2.1	0.18
11	Ophiuroids	2	1.5	0.13
12	Tunicates	2	1.5	0.13
13	Isopods	2	0.9	0.08
14	Fish eggs	2	0.6	0.05
15	Caprellid amphipods	2	0.4	0.03
16	Pagurid crabs	2	0.4	0.03
17	Foraminiferans	1	0.2	<0.01
18	Sipunculid introverts	1	0.2	<0.01
19	Fish	1	0.2	<0.01
20	Unidentified eggs	1	<0.1	<0.01
Also,	crustacean fragments	11	9.4	4.31
	Algae fragments	8	11.5	3.83
	Unidentified material	15	31.5	19.69

TABLE 53.—Food of *Thalassoma fuscus*.

Rank	Items	No. fish with this item (n = 14)	Mean percent of diet volume	Ranking index
1	Brachyuran crabs	7	35.5	17.75
2	Mollusks	5	17.2	6.14
3	Octopods	1	7.1	0.51
4	Ophiuroids	1	5.0	0.36
5	Polychaetes	2	1.8	0.26
6	Sipunculid introverts	2	1.4	0.20
7	Crab megalops	1	2.8	0.20
8	Fish	1	2.5	0.18
9	Gammaridean amphipods	3	0.7	0.15
10	Cyclopoid copepods	3	0.6	0.13
11	Calanoid copepods	1	1.4	0.10
12	Isopods	1	0.1	<0.01
Also, crustacean fragments		2	3.7	0.53
	Unidentified fragments	8	20.2	11.54

TABLE 54.—Food of *Halichœres ornatissimus*.

Rank	Items	No. fish with this item (n = 13)	Mean percent of diet volume	Ranking index
1	Mollusks	6	13.5	6.23
2	Gammaridean amphipods	7	7.7	4.15
3	Colonial diatoms	4	6.9	2.12
4	Didemnid tunicates	3	8.8	2.03
5	Tanaids	5	1.5	0.58
6	Harpacticoid copepods	4	1.7	0.52
7	Sipunculid introverts	3	1.2	0.28
8	Ophiuroids	1	3.1	0.24
9	Cyclopoid copepods	2	0.8	0.12
10	Polychaetes	1	1.5	0.12
11	Isopods	2	0.5	0.08
12	Demersal eggs	1	0.8	0.06
13	Echinoids	1	0.4	0.03
14	Ostracods	1	0.1	<0.01
Also, crustacean fragments		7	10.8	5.82
	Sand and foraminiferans	3	4.5	1.04
	Algal fragments	2	1.2	0.18
	Unidentified fragments	10	35.0	26.92

The widespread occurrence of this fish probably relates to the fact that no single item, or certain few items, especially predominate in its diet. This is true to an even greater degree in the ubiquitous *Thalassoma duperrey*, above, but is unlike most fishes on Kona reefs.

CONCLUSION.—*Halichoeres ornatissimus* is a diurnal predator that picks a wide variety of small benthic animals from the sea floor.

Stethojulis balteata (Quoy and Gaimard) — *'omaka*

This wrasse is most numerous on the shallow reef flats and on some of the reefs richly overgrown with corals. During the day it swims close to rocks or coral, at which it periodically picks. At night it rests in reef crevices, or buried in the sand.

All five specimens (90: 76-102 mm) collected during daylight had a gut full of material, some of it fresh, as listed in Table 55. The major food items—small crustaceans shorter than about 4 mm—were mostly intact. Larger items, such as some of the gastropods, were crushed.

CONCLUSION.—*Stethojulis balteata* is a diurnal predator that mostly picks small crustaceans and gastropods off the sea floor.

Anampses cuvier Quoy and Gaimard—*'opule*

Although this wrasse occupies all inshore reef habitats in Kona, it is most numerous where the sea floor consists of basalt boulders. During the day, solitary individuals swim close to the substratum, where they inspect the surface, and frequently pluck at the low growth of algae on the

TABLE 55.—Food of *Stethojulis balteata*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Harpacticoid copepods	5	19.4	19.40
2	Prosobranch gastropods	4	15.6	12.48
3	Gammaridean amphipods	3	8.6	5.16
4	Tanaids	3	5.0	3.00
5	Foraminiferans	2	2.4	0.96
6	Isopods	2	2.4	0.96
7	Polychaetes	1	4.0	0.80
8	Echinoids	1	1.0	0.20
9	Sipunculid introverts	1	0.6	0.12
10	Cyclopoid copepods	1	0.4	0.08
Also, crustacean fragments		5	15.0	15.00
	Sand and debris	4	10.2	8.16
	Unidentified fragments	4	15.4	12.32

TABLE 56.—Food of *Anampses cuvier*.

Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Gammaridean amphipods	10	28.9	24.08
2	Mollusks	10	18.1	15.08
3	Polychaetes	3	4.3	1.08
4	Xanthid crabs	3	1.8	0.45
5	Fish eggs, demersal	1	5.0	0.42
6	Echinoids	2	1.9	0.32
7	Tanaids	3	0.3	0.08
8	Isopods	3	0.3	0.08
9	Didemnid tunicates	2	0.3	0.05
Also, crustacean fragments		9	14.1	10.58
	Sand and foraminiferans	4	4.3	1.43
	Algal fragments	3	1.9	0.48
	Unidentified fragments	8	18.8	12.53

rocks. Much sand has accumulated here, and periodically they pause during their foraging to blow a small cloud of sand and debris from their mouths. At night this wrasse is out of sight, presumably resting in reef crevices.

All 12 specimens (169: 110-225 mm) speared during daylight had a gut full of material, much of it fresh, as listed in Table 56. The gammaridean amphipods, all shorter than 3 mm, were the major prey of even the largest individuals. Furthermore, the mollusks, which were the only other significant prey, were mostly prosobranch gastropods also shorter than 3 mm.

Undoubtedly, the small size and other characteristics of these prey are reflected in the feeding morphology of *A. cuvier* and its congeners, certain features of which set them apart from most other labrids in Kona. In dentition, the species of *Anampses*, with two flattened teeth projecting forward from the front of each jaw, are unlike those of any other genus of Hawaiian fishes (Gosline and Brock, 1960). Obviously this specialized dentition effectively captures gammarideans that inhabit the low stubble of algae overgrowing most basalt boulders. Compared with most other labrids, species of *Anampses* have the pharyngeal teeth reduced, which is expected considering the relatively small proportion of crushed items in the diet. The food items are mostly so small they need not be crushed upon ingestion. Gammarideans and certain other prey of similar size regularly pass intact through the pharynx of even those labrids with well-developed pharyngeal teeth (see accounts of other labrids in this report).

CONCLUSION.—*Anampses cuvier* is a diurnal predator that mostly plucks small benthic organisms, especially gammarideans, from rocky substrata.

Coris gaimard (Quoy and Gaimard)—*hinalea lolo*

This wrasse is most numerous where the reef is interspersed with small patches of sand. It forages in this sand during daylight, usually close to the base of rock or coral. Of all the wrasses treated in this report, this one is the most adept at excavating buried organisms. Moving its head sidewise, it effectively overturns small stones or digs in the

TABLE 57.—Food of *Coris gaimard*.

Rank	Items	No. fish with this item (n = 9)	Mean percent of diet volume	Ranking index
1	Mollusks	9	72.2	72.20
2	Echinoids	3	9.8	3.27
3	Crabs	1	2.2	2.44
4	Didemnid tunicates	1	0.6	0.07
5	Gammaridean amphipods	1	0.2	0.02
Also, crustacean fragments		5	15.0	8.33

TABLE 58.—Food of *Macropharyngodon geoffroy*.

Rank	Items	No. fish with this item (n = 8)	Mean percent of diet volume	Ranking index
1	Prosobranch gastropods	8	37.8	37.80
2	Foraminiferans	8	35.3	35.30
3	Harpacticoid copepods	2	0.4	0.10
4	Gammaridean amphipods	1	0.1	0.01
Also, crustacean fragments		2	0.6	0.15
	Sand and algae	5	8.4	5.25
	Unidentified fragments	6	17.4	13.05

sand, exposing hidden prey. It is not seen at night, when presumably it is buried in the sand, or secreted in reef crevices.

All nine specimens (117: 81-164 mm), speared during daylight, contained relatively fresh material, but items longer than a few millimeters were crushed so extensively that precise identifications were difficult. The gut contents are itemized in Table 57.

CONCLUSION.—*Coris gaimard* is a diurnal predator that mostly excavates mollusks and other prey that are buried in the sand.

Macropharyngodon geoffroy (Quoy and Gaimard)

This solitary little wrasse is widespread on Kona reefs, but is nowhere numerous. It swims close among coral and rocks during daylight, but is not seen after dark, when presumably it secretes itself in reef crevices, or under the sand.

All eight specimens (99: 74-120 mm) collected during the day had the gut full of the items listed in Table 58, almost all crushed.

The exceptionally large pharyngeal teeth of this wrasse obviously are adapted to a diet of heavily shelled organisms. The specimens examined, which had fed mostly on gastropods and foraminiferans, are undoubtedly representative. The foraminiferans were almost all *Marginospora vertebralis*, which is an abundant benthic form on shallow reefs in the Marshall Islands (Cushman, Todd, and Post, 1954).

CONCLUSION.—*Macropharyngodon geoffroy* is a diurnal predator that feeds mostly on benthic gastropods and foraminiferans.

Gomphosus varius Lacépède—bird wrasse, *hinalea 'i'iwi*

This wrasse is numerous on shallow surge-swept reefs, especially where the coral *Pocillopora meandrina* abounds. During daylight solitary individuals swim among the coral heads, probing with their elongated snouts among the coral branches. At night the species lies quietly in reef crevices.

All 12 specimens (142: 114-180 mm) collected during the day had their guts full of the items listed in Table 59. Most of this material was crushed. The xanthid crabs were mostly *Trapezia* sp. They and the alpheids are species that live among the branches of *P. meandrina*. Hiatt and Strasburg (1960) noted that this labrid's major prey in the Marshall Islands are xanthids and alpheids that live in the interstices of ramose corals. Randall (1955) similarly reported alpheid shrimps and also stomatopods in the diet of this species (as *G. tricolor)* in the Gilbert Islands.

Gomphosus varius takes relatively large motile prey, and with its large mouth does not pluck them from the substratum in the manner characteristic of the many other wrasses that prey on relatively tiny or sessile organisms. Rather, this wrasse vigorously wrests its prey from the reef crevices in which they are secreted.

TABLE 59.—Food of *Gomphosus varius*.

Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	7	37.9	22.11
2	Alpheid shrimps	2	6.7	1.12
3	Pelecypods	1	4.2	0.35
4	Gastropods	2	2.1	0.35
Also, crustacean fragments		8	25.8	17.20
	Unidentified fragments	4	23.3	7.77

CONCLUSION.—*Gomphosus varius* is a diurnal predator that takes relatively large crustaceans from reef crevices.

General Remarks on Wrasses

Kona reefs, like tropical reefs the world over, are populated by a diverse array of wrasses, most of them with strong pharyngeal teeth adapted to crush hard-bodied prey. *Macropharyngodon geoffroy*, for example, preys on more heavily armored prey—in this case mollusks and foraminiferans. Others, like *Anampses cuvier*, have the pharyngeal teeth less developed and prey mostly on tiny crustaceans. Some of the wrasses, especially *Thalassoma duperrey*, are highly opportunistic, and these tend to be the most widespread and have the most varied diets.

It is well known that wrasses are active only during the day; at night they rest in reef crevices and under the sand (Longley and Hildebrand, 1941; Gosline and Brock, 1960; Hobson, 1965, 1968a, 1972; Starck and Davis, 1966; Collette and Talbot, 1972). They are among the first diurnal fishes on the reef to seek cover at day's end, and among the last to leave cover in the morning (Hobson, 1965, 1968a, 1972; Collette and Talbot, 1972).

Family Scaridae: parrotfishes

Scarus sordidus Forskål—*uhu*

This is one of the more numerous parrotfishes in Kona, especially over coral-rich reefs. During the day, it swims actively close to the substratum, often in groups. With its parrotlike beak, it scrapes away the fine filamentous algae that grows over the surface of dead coral, especially *Porites*. Although frequently it scrapes up to the edge of living coral, it stops there (Figure 34). During twilight, this species migrates in schools from one part of the reef to another, but the migratory pattern remains unclear (Hobson, 1972).

At night *S. sordidus* rests solitarily in reef crevices. Because some parrotfishes are known to secrete a mucous envelope around themselves at night (Winn, 1955), during a series of night observations over 3 mo I estimated the standard length of each resting parrotfish, and noted whether or not it was encased in mucus. During these observations, 20 individuals of this species were seen, estimated to be between 150 and 350 mm long. All eight that appeared to be shorter than 300 mm were in mucous envelopes, whereas all six without envelopes were judged to be longer than 300 mm. The other six, all estimated to exceed about 300 mm long, were in envelopes. Thus, all the smaller individuals, but only some of the larger ones, were in envelopes.

The guts of all seven *S. sordidus* (195: 150-213 mm) that were speared during midday were full of bits of algae, mixed with calcareous powder, organic slurry, and sand (proportions undetermined, but the algae constituted less than 20%). No evidence was found in these specimens of coral tissues or mucus (the latter is prominent in the gut contents of fishes known to feed on coral), even though Hiatt and Strasburg (1960) reported that coral polyps constituted the major food of this parrotfish in the Marshall Islands. These authors stated (p. 103): "Scraping living coral heads seems to be its predominant mode of feeding." This observation contrasts with mine in Kona, where *S. sordidus* avoids the living coral when feeding.

CONCLUSION.—*Scarus sordidus* is a diurnal herbivore that feeds mostly by scraping fine benthic algae that have overgrown the surface of dead coral.

Scarus taeniurus Valenciennes—*uhu*

My observations of their social interactions render it clear that the two forms Schultz (1969) distinguished in Hawaii as *S. taeniurus* and *S. forsteri* are conspecific and that his *"S. forsteri"* represents the large male of the species.

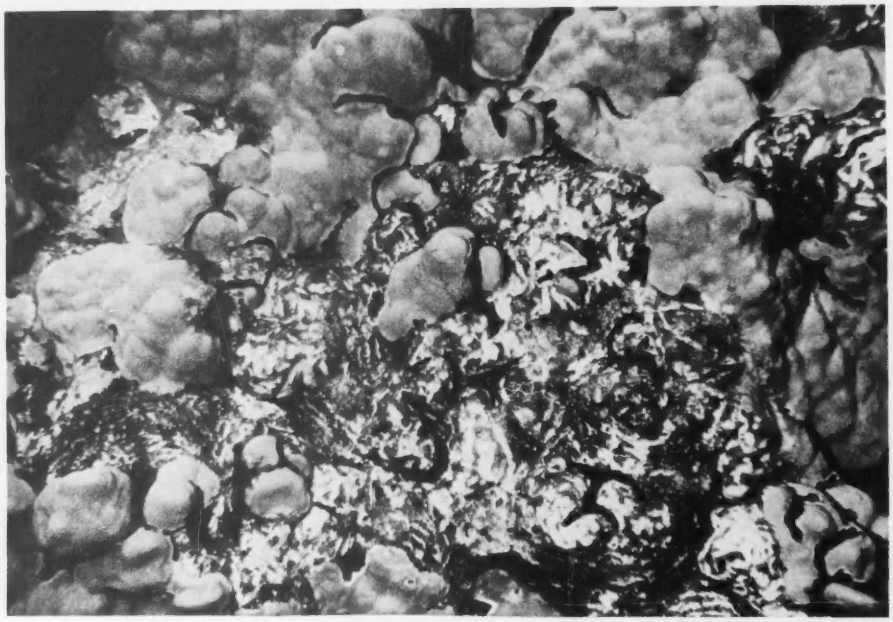

FIGURE 34.—Area of the reef showing scrape marks made by the teeth of grazing parrotfishes, mostly *Scarus sordidus*. Note that grazing has occurred only where dead coral is overgrown with algae—no living coral has been scraped.

This, the smallest Hawaiian species of *Scarus* (not exceeding a length of about 300 mm), is by far the most numerous parrotfish over exposed basalt on shallow reef flats and adjacent reef faces. The smaller juveniles and females, usually in aggregations, tend to occupy the shallow flats, the larger, distinctively hued males, which are usually solitary, tend to occupy the reef faces. This species is like *S. sordidus* in grazing during the day; however, whereas *S. sordidus* usually scrapes algae from the surface of dead coral, *S. taeniurus* ordinarily scrapes algae from the surface of rocks.

At night *S. taeniurus* rests in reef crevices. During the series of night observations in which I checked the incidence of mucous envelopes, all 11 *S. taeniurus*, which were less than 300 mm long, were in envelopes (Figure 35).

The two individuals (150 and 243 mm) that were collected during midday were full of bits of algae, mixed with calcareous powder, organic slurry, and sand (proportions undetermined, but the algae made up less than 20%), with no evident trace of coral tissue or mucus.

CONCLUSION.—*Scarus taeniurus* is a diurnal herbivore that usually feeds by scraping benthic algae from rock surfaces.

Scarus rubroviolaceus Bleeker—*uhu palukaluka*

During the day this parrotfish ranges over the reef, usually in mixed groups of several males and females. It occurs on all the inshore reefs, but mostly on rock substrata. Generally, using the sides of its jaws, it takes one bite and then withdraws a few centimeters before approaching for another bite.

At night *S. rubroviolaceus* rests in reef crevices. While surveying the incidence of mucous envelopes in resting parrotfishes (see accounts for *S. sordidus* and *S. taeniurus* above), of the nine *S. rubroviolaceus* that were observed, including both males and females approximately 200 to 500 (mean 394) mm long, none were in envelopes (Figure 36). Because the large and distinctive males of *S. rubroviolaceus* are not numerous, I came to recognize some individuals. These often returned

FIGURE 35.—*Scarus taeniurus*, a parrotfish, resting in a mucous envelope at night, a habit apparently shared by all members of this relatively small species.

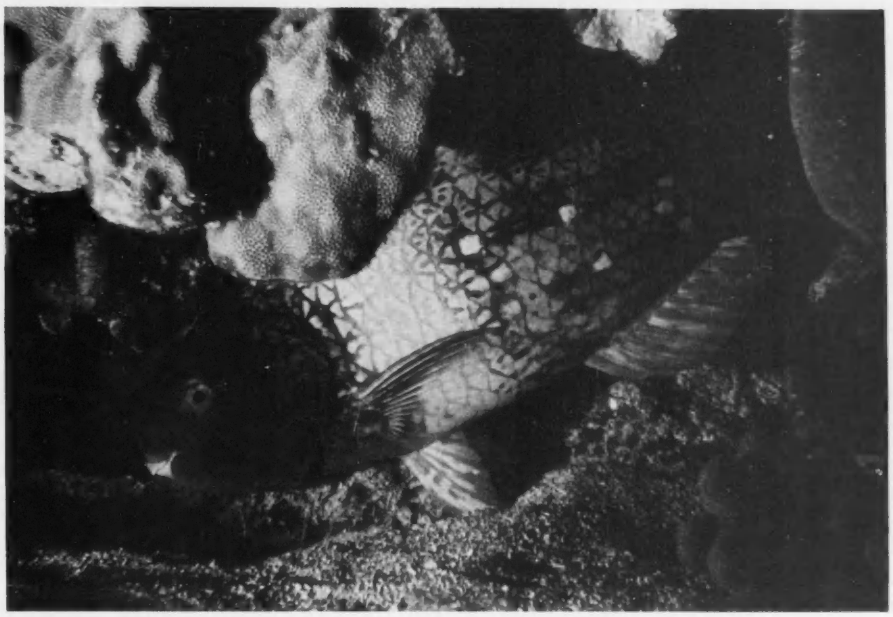

FIGURE 36.—*Scarus rubroviolaceus*, female, a parrotfish, resting under a ledge at night. Members of this species were never seen in mucous envelopes.

night after night to caves in the same areas, but not necessarily to the same cave, as has been reported for some parrotfishes elsewhere (e.g. Winn and Bardach, 1960; Starck and Davis, 1966).

The guts of two males (340 and 410 mm) that were speared during midday were full of bits of algae mixed with calcareous powder, organic slurry, and sand (proportions undetermined, but the algae constituted less than 20%), with no evident trace of coral tissue or mucus.

CONCLUSION.—*Scarus rubroviolaceus* is a diurnal herbivore that typically scrapes benthic algae from rock surfaces.

General Remarks on Parrotfishes

It is well known that parrotfishes are quiescent at night. They have been thus described in the tropical Atlantic (Winn, 1955; Winn and Bardach, 1959, 1960), eastern Pacific (Hobson, 1965; Rosenblatt and Hobson, 1969), Hawaii (Hobson, 1972), and elsewhere. Earlier (Hobson, 1965), I suggested that mucous envelopes in resting parrotfishes at night are characteristic of certain small individuals, or of individuals suffering injury or stress. The relation between small size and envelope secretion was also noted by Starck and Davis (1966) and by Casimir (1971). Winn and Bardach (1959) believed that the envelope is a defense against nocturnal predators, especially those that sense prey by olfaction or gustation, as do certain moray eels (Bardach, Winn, and Menzel, 1959). Because the threat from predators increases with decreasing size, obviously the smaller individuals are in greatest need for protection. Similarly, it is known that injured or distressed fishes are particularly attractive to predators (e.g. Hobson, 1968a), so envelope secretion by parrotfishes suffering these conditions is consistent with the idea that the envelopes provide protection. The survey of mucous envelopes in Kona shows a decreasing incidence with increasing size. Nevertheless, Winn and Bardach (1960), working with *Scarus vetula* at Bermuda, found that certain individuals in aquaria produced the envelope irregularly, and Smith and Tyler (1972) found that one individual of that species observed on a reef in the Virgin Islands formed an envelope on some nights, but not on others. Probably this variation within individuals occurs in other species too, but the question was not examined in Kona, where only certain males of *S. rubroviolaceus* were recognized as individuals, and these were never seen in envelopes.

There is controversy over the diet of parrotfishes. Hiatt and Strasburg (1960) reported a diet of living coral not only in *S. sordidus*, as noted above, but also in all other scarids they examined in the Marshall Islands. I found no evidence that any of the species in Kona, including *S. sordidus*, feed on living coral. Randall (1967) similarly concluded that parrotfishes in the West Indies do not feed on living coral; he noted the large amount of sand in the guts of parrotfishes, and suggested that this material, taken purposefully, aids in grinding plant tissue—the primary food—in the pharyngeal mill.

Although I classify all parrotfish species in Kona as herbivores, their large gut loads of calcareous powder, organic slurry, and sand seem too great a proportion of the total contents to have been taken only incidentally, or to be adaptive only because it aids in grinding up plant tissue. There is need to look closer at how parrotfishes utilize the material they ingest.

Family Blenniidae: combtooth blennies

The combtooth blennies are most numerous in tide pools and close to rocky shores, where frequently they are the dominant fishes. However, this report considers only those species that occur regularly in water deeper than 5 m.

Exallias brevis (Kner)—*pao'o kauila*

Because *E. brevis* is distinctively hued and habitually perches in exposed positions during the day (Figure 37), it is frequently noticed even though it is not especially numerous. It rarely leaves the sea floor and usually rests immobile except when scraping the surface of living coral with its comblike teeth. After dark, it is secreted in reef crevices and seen only occasionally.

Of the 10 specimens (94: 70-106 mm) examined, 2 that were taken from under partial cover at night (between 4 and 5 h after sunset) contained only well-digested fragments, whereas only 1 taken during the day was empty, and the other 7 were full of food, including fresh material. The major item in all seven (over 90% of the contents in each) was scleractinian corals—both skeletal and tissue fragments, along with much mucus. The remaining identifiable items in the diet were fine filamentous algae and diatoms.

FIGURE 37.—*Exallias brevis*, a blenny, showing typical diurnal attitude.

In contrast to these food data, Hiatt and Strasburg (1960) found only filamentous algae and detritus in the single *E. brevis* (80 mm) that they examined in the Marshall Islands.

CONCLUSION.—*Exallias brevis* is a diurnal species that feeds largely on scleractinian corals, both tissue and mucus.

Cirripectus variolosus (Valenciennes)

During the day, this relatively small blenny moves about close to cover on the reef, remaining in contact with the substratum. Though numerous, it is not seen after dark, when presumably it is secreted in reef crevices.

The guts of both specimens (66 and 80 mm) collected during midday contained filamentous algae (about 40% of the diet volume) and what appeared to be detritus (50 to 60%). In addition, one contained a few scleractinian coral fragments (5%). Except for the coral fragments, the diet of these two individuals was the same as that of one specimen of this species examined by Hiatt and Strasburg (1960) in the Marshall Islands.

CONCLUSION.—*Cirripectus variolosus* is a diurnal species that feeds mostly on algae and detritus.

Plagiotremus goslinei (Strasburg)—sabre-toothed blenny

During the day, *P. goslinei* hovers a meter or so above the reef, from which position it attacks larger fishes that incidentally pass by, striking them unseen from below and behind, much as does *P. azalea* in the eastern Pacific (Hobson, 1968a, 1969). But whereas *P. azalea* usually aggregates when hovering above the reef, *P. goslinei* usually is solitary. No specimens of *P. goslinei* were collected, but presumably it feeds on the mucus and dermal tissue of its victim, as do other species of this genus, including *P. rhinorhynchus* (Wickler, 1960), *P. azalea* (Hobson, 1968a), and *P. townsendi* (Springer and Smith-Vaniz, 1972). These species are called sabre-toothed blennies because each carries in its lower jaw a pair of enormous fangs. Eibl-Eibesfeldt (1955) and Strasburg (1960) believed that these fangs are used in feeding, but Wickler (1960) concluded from work in aquaria

that *P. rhinorhynchus* uses its fangs not to feed, but rather to defend its territory.

Plagiotremus goslinei hovers above the reef during only part of the day. Much of the time it occupies abandoned mollusk and worm tubes on the rocks, and these retreats also serve as resting places at night. In the eastern Pacific, *P. azalea* uses similar tubes in the same way (Hobson, 1968a, 1969).

CONCLUSION.—*Plagiotremus goslinei* is a diurnal predator that feeds on mucus and dermal tissue of larger fishes.

General Remarks on Combtooth Blennies

The combtooth blennies are generally regarded as diurnal. For example, Starck and Davis (1966) did not see members of the family, known to be present, during many night observations on Florida reefs, and Randall (1967) reported the group to be diurnal in the West Indies.

Although food habits remain unknown or uncertain for most combtooth blennies, reportedly many feed by scraping filamentous algae and detritus from rocks. These items predominated in the diet of all four blenniid species that Randall (1967) examined in the West Indies, and in all five studied by Hiatt and Strasburg (1960) in the Marshall Islands. In Kona, this mode of feeding occurs in *Cirripectus variolosus*, but *Exallias brevis* may be exceptional in feeding mostly on the tissue and mucus of scleractinian corals. The significance of coral mucus as food of *E. brevis* may relate to the significance of fish mucus as food for blennies of the genus *Plagiotremus*. Böhlke and Chaplin (1968) suggested that at least some combtooth blennies which scrape algae from rocks may gain most of their nourishment from small organisms living on or around the algae. Clearly, much about blenniid feeding remains unknown. Because these small fishes scrape their food from various substrata, their gut contents are difficult to analyze. One can easily see that species of *Plagiotremus* have a mode of feeding that differs from those of other blenniids, because their manner of taking food is uniquely spectacular. In comparison, differences distinguishing the feeding modes of other combtooth blennies are relatively subtle.

Family Acanthuridae: surgeonfishes

The surgeonfishes are the predominant fishes over most Hawaiian inshore reefs, but this report treats only the two species that feed on zooplankton in the water column. The habits of these two were only superficially touched on by Jones (1968), who provided a thorough treatment of the many species occurring in Kona that take their food directly from the substratum (see general remarks on surgeonfishes, below).

Acanthurus thompsoni (Fowler)

Acanthurus thompsoni (Figure 38) swims in stationary aggregations in the water column above the reef in several locations along the outer drop-off, 20 to 30 m deep. Often mixed with this surgeonfish in these groups are several other species, especially *Chromis verater*, *C. ovalis*, and *Naso hexacanthus*. At nightfall, *A. thompsoni* descends to the reef below where, inactive but alert, it remains under cover until morning.

Fourteen individuals (141: 128-185 mm) were speared at different times of day and night. All six that were taken from crevices during the hour before daybreak had empty stomachs, whereas, all seven collected from aggregations in the water column at various times during afternoons had full stomachs, including fresh material. Finally, one solitary individual speared during midafternoon close among the coral in about 6 m of water, approximately 200 m from the nearest feeding aggregation, had its stomach empty. The seven individuals with material in their stomachs contained the items listed in Table 60.

The data show a strong trend in the diet toward relatively large, semitransparent, and often gelatinous prey. Some planktivorous fishes from other families feed heavily on one or another of these prey, as does the pomacentrid *Chromis verater*, which feeds heavily on larvaceans (see species account, above). But in none of these others is the diet similarly dominated by an array of such prey. However, the sparse information on the food habits of *A. thompsoni* given by other authors does not show this trend. Gosline and Brock (1960) reported only mollusk eggs and copepods, whereas Jones (1968) noted copepods, crab zoea, crab megalops, and mysids. But these reports did not indicate how many specimens were examined, nor the relative proportion of each type of prey in the diet. Most important, they did not indicate how much of the gut contents remained unidentified. The major food items that I found in *A. thompsoni* are types quickly rendered unidentifiable by digestion, and thus easily missed if the sample is not fresh.

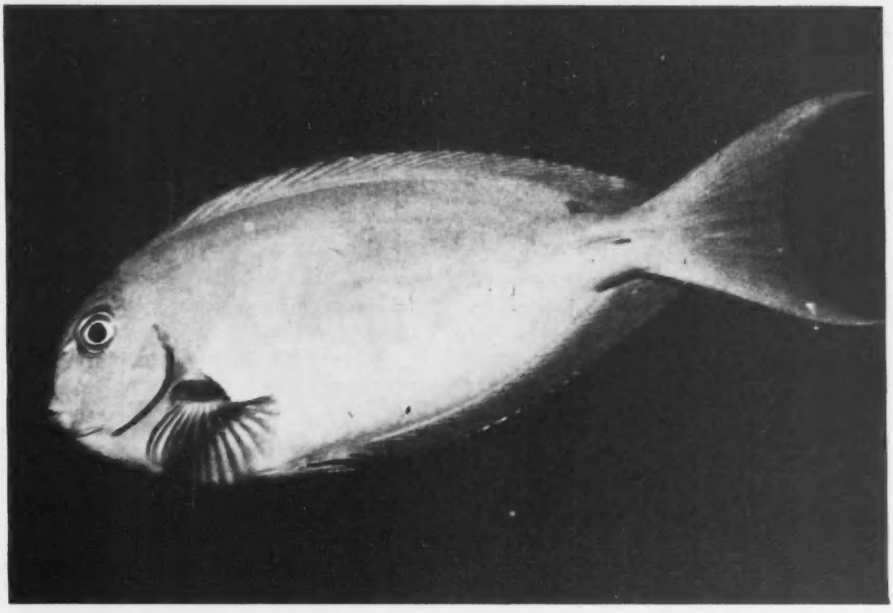

FIGURE 38.—*Acanthurus thompsoni*, a zooplanktivorous surgeonfish. In comparison with its bottom-feeding congeners, this species carries its more upturned mouth higher on its head, its body is more fusiform, and its tail is more deeply lunate. These morphological tendencies occur in many unrelated zooplanktivorous fishes.

CONCLUSION.—*Acanthurus thompsoni* is a diurnal planktivore that feeds mostly on semi-transparent, often gelatinous, organisms—especially chaetognaths, salps, siphonophores, and larvaceans.

Naso hexacanthus (Bleeker)—*kala*

During daylight, this relatively large surgeonfish swims above the outer drop-off in schools that periodically range farther offshore to yet unknown distances. Brock and Chamberlain (1968) found this species at depths below 120 m when diving in the research submarine *Asherah*, but it is not known whether these fish had migrated from shallower water or are of deepwater populations, although the latter possibility seems the more probable. Generally, individuals in less than 10 m of water over inshore reefs during the day are relatively small, and swim in groups of

TABLE 60.—Food of *Acanthurus thompsoni*.

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Chaetognaths	6	37.1	31.80
2	Salps	7	18.6	18.60
3	Siphonophores	4	10.0	5.71
4	Larvaceans	5	7.4	5.29
5	Calanoid copepods	4	8.6	4.91
6	Gelatinous egg masses	2	1.7	0.49
7	Gelatinous clumps of blue-green algae	2	1.6	0.46
8	Fish eggs, planktonic	2	1.3	0.37
9	Hyperiid amphipods	3	0.7	0.30
10	Polychaetes	2	0.9	0.26
11	Decapod shrimps	1	0.3	0.04
12	Harpacticoid copepods	1	0.1	0.01
Also, unidentified fragments		4	11.7	6.69

only a few individuals, often close to the substratum. Most representatives seen inshore are not feeding, but rather move uniformly together closely spaced in schools. When they do feed, the schools are abandoned for aggregations in which loosely spaced individuals act independently.

During evening twilight many individuals move in from deeper water over the shallower parts of the reef. Larger representatives are in the shallows only after dark. On dark nights, the species is scattered close among rocks and corals, relatively inactive, but alert. However, on moonlit nights some swim above the reef in small groups.

Sixteen individuals (261: 202-392 mm) were speared at various times of night and day. Because larger individuals are less accessible, especially during the day, the sample is biased toward smaller members of the species. All four solitary individuals taken close among rocks or coral at night (later than 4 h after sunset and before daybreak) had empty stomachs, whereas only one of nine others taken from schools above the reef at various times of day had material in its stomach, and this one came from a school that had just appeared over the reef from offshore during midafternoon. Finally, all three that had been observed feeding when speared above inshore reefs (on three afternoons over 2 mo) had full stomachs. Items in the four individuals whose stomachs contained food are listed in Table 61.

Like *Acanthurus thompsoni*, this acanthurid feeds mostly on semitransparent, often gelatinous, prey. Of the four that contained food, the three taken from inshore feeding aggregations were relatively small fish (233-238 mm) whose major food was planktonic fish eggs. Perhaps significantly, there were no fish eggs in the fourth specimen, which had just appeared over the reef from offshore. This individual was larger than the others, about 300 mm long, but was collected within 30 min of one of them. The major item in its stomach was filamentous red algae, which did not occur in the smaller three. Only chaetognaths and larvaceans occurred in the stomachs of all four specimens. These limited data suggest there may be distinctive differences in diet and feeding grounds over the size range of individuals sampled.

The high incidence of empty stomachs among individuals over the inshore reefs during the day, as well as at night, suggests that many may feed offshore, and be relatively inactive, or at least not feeding, when they are inshore.

Jones (1968) included *N. hexacanthus* with *A. thompsoni* when reporting the diet of copepods, crab zoea, crab megalops, and mysids noted above. My comments concerning the reported diet of *A. thompsoni* (see above) apply equally here.

CONCLUSION.—*Naso hexacanthus* is a diurnal planktivore that takes mostly semitransparent, often gelatinous, prey—especially chaetognaths, larvaceans, and fish eggs. Limited data suggest that drifting pieces of filamentous algae may also be important.

General Remarks on Surgeonfishes

Surgeonfishes are widespread on tropical reefs, and usually are described in a general way as herbivores (e.g. in the Bahamas by Böhlke and Chaplin, 1968; and in the West Indies by Randall, 1967). Jones (1968) grouped the many Hawaiian surgeonfishes according to their habitats and methods of foraging. In categorizing the bottom-foraging species, not studied by me, he defined three types of habitats, and listed the surgeonfishes characteristic of each: 1) The turbulent

TABLE 61.—Food of *Naso hexacanthus*.

Rank	Items	No. fish with this item (n = 4)	Mean percent of diet volume	Ranking index
1	Chaetognaths	4	21.3	21.30
2	Fish eggs, planktonic	3	25.0	18.75
3	Larvaceans	4	16.3	16.30
4	Filamentous red algae	1	18.4	4.60
5	Decapod shrimps	3	2.3	1.73
6	Calanoid copepods	2	2.3	1.15
7	Siphonophores	2	2.0	1.00
8	Polychaetes	1	1.3	0.33
9	Hyperiid amphipods	1	0.5	0.13
10	Mollusk veligers	1	0.3	0.08
11	Gammaridean amphipods	1	0.3	0.08
Also, unidentified fragments		2	10.0	5.00

waters of the surge zone are frequented by four species of *Acanthurus* (*achilles, glaucopareius, guttatus,* and *leucopareius*). 2) The sand patches on deeper, more tranquil reefs are home to four species of *Acanthurus* (*dussumieri, mata, olivaceus,* and *xanthopterus*). 3) Finally, basalt and coral substrata on reefs below the surge zone (to a depth of about 90 m) are inhabited by three species of *Acanthurus* (*nigrofuscus, nigroris,* and *sandvicensis*); two species of *Ctenochaetus* (*hawaiiensis* and *strigosus*); two species of *Zebrasoma* (*flavescens* and *veliferum*; the adults of the latter often occur in the surge zone); and three species of *Naso* (*brevirostris, lituratus,* and *unicornis*).

In erecting categories according to foraging types, Jones (1968) classified the bottom feeders either as browsers or grazers. The browsers are described as "strictly herbivores that bite and tear off bits of multicellular benthic algae, generally without ingesting any of the inorganic substratum." Browsing surgeonfishes include those characteristic of the surge zone and those characteristic of subsurge reefs, except for the two *Ctenochaetus*. The browsing species of *Acanthurus* and *Zebrasoma* feed chiefly on fine filamentous algae, whereas the browsing species of *Naso* tend to feed on the leafy and fleshy forms.

Surgeonfishes classified by Jones (1968) as grazers are described as "Fishes that purposely pick up large quantities of the substratum while feeding. . . irrespective of whether the material is rasped away from rocks, or picked up as loose sand." This category includes the surgeonfishes characteristic of the sand patches, all of which are species of *Acanthurus,* and the two reef-dwelling species of *Ctenochaetus*. The sand-patch *Acanthurus* species pick up mouthfuls of sand, whereas the reef-dwelling *Ctenochaetus* species ingest sediment that has accumulated over rocks and dead coral. In examining these sediment-packed guts, Jones found material from the two groups distinguishable by particle size—being coarse and grainy in the sand-patch *Acanthurus,* fine and silty in the reef *Ctenochaetus*. He concluded that the major food of both groups are diatoms and detritus that have accumulated around the particles in the surface layers of the sediment.

Surgeonfishes are widely recognized to be active by day and relatively inactive at night (e.g. in the Gulf of California by Hobson, 1965; and in the Florida Keys by Starck and Davis, 1966). Although quiescent, these nocturnally resting acanthurids are most often described as alert; however, Collette and Talbot (1972) reported that *Acanthurus coeruleus* sleeps while sheltered among coral at night in the Virgin Islands. In the Gulf of California, *Prionurus punctatus* aggregates above the reef on bright moonlit nights (Hobson, 1965), as does *Naso hexacanthus* in Kona.

Family Zanclidae: moorish idol

Zanclus canescens (Linnaeus)—moorish idol, *kihikihi*

The moorish idol (Figure 39a) is closely related to the surgeonfishes, and some ichthyologists (e.g. Greenwood et al., 1966) consider it to be a member of that family. It lacks the caudal spine common to all surgeonfishes, however, and most classifications assign it to the monotypic family Zanclidae.

This fish is numerous in all Kona inshore habitats, where it swims over the reef during the day, usually in groups of four to six individuals. When feeding, it regularly probes the narrow cracks and crevices of the reef with its elongated snout. At night it is relatively inactive, but alert, close among rocks or coral, and at this time its coloration differs strikingly from that displayed in daylight (compare Figure 39a and b).

Of 21 specimens (108: 74-137 mm) speared at various times of day and night, all 9 that were collected at night (later than 4 h after sunset and before sunrise) had empty stomachs, whereas all 12 that were taken during the day (between midmorning and late afternoon) had full stomachs that included fresh material. Items in the specimens containing identifiable material are listed in Table 62.

The sponges, which greatly predominate in the diet, were all small species that presumably live in narrow reef crevices. This fish appears to be specialized in this diet, although Randall (1955) reported only algae in two specimens from the Gilbert Islands.

CONCLUSION.—*Zanclus canescens* is a diurnal species that feeds mostly on small sponges.

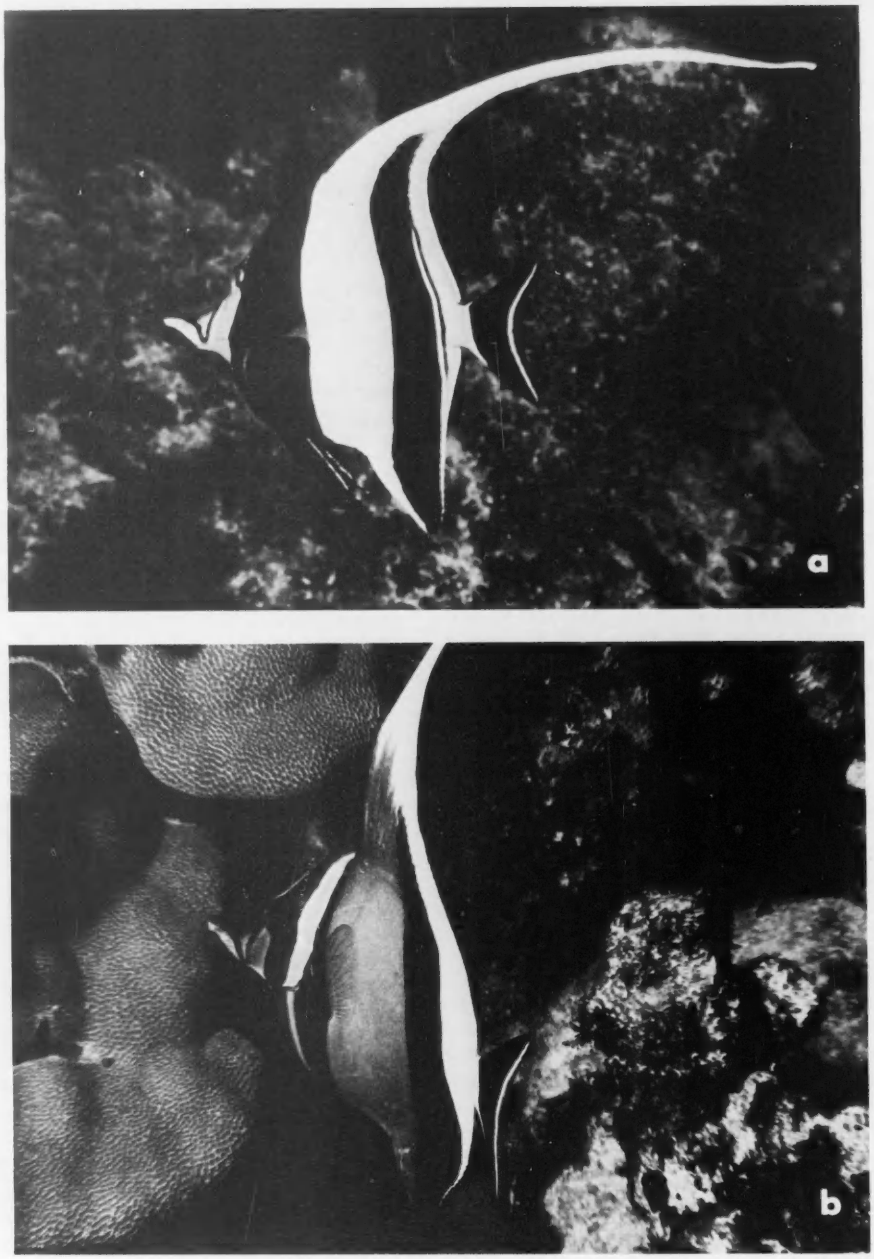

FIGURE 39.—*Zanclus canescens*, the moorish idol: a, showing diurnal coloration while swimming over the reef during the day; b, showing nocturnal coloration while close to the reef at night.

TABLE 62.—Food of *Zanclus canescens*.

Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Sponges	12	84.5	84.50
2	Coralline algae	12	5.7	5.70
3	Other algae	12	5.6	5.60
4	Bryozoans	8	1.1	0.73
5	Pelecypod mollusks	8	0.9	0.60
6	Gammaridean amphipods	6	0.5	0.25
7	Polychaetes	4	0.6	0.20
8	Foraminiferans	3	0.3	0.08
9	Hydroids	2	0.2	0.03
10	Barnacle cirri	2	0.2	0.03
11	Didemnid tunicates	1	0.2	0.02
12	Tanaids	1	0.1	<0.01
13	Decapod shrimps	1	0.1	<0.01

ORDER PLEURONECTIFORMES

Family Bothidae: left-hand flounders

Bothus mancus (Broussonet)—*paki'i*

This flatfish is most numerous lying immobile where rocks are interspersed with small patches of sand. It changes its coloration to match closely that of whatever substratum it happens to lie on, rocks or sand. When on sand, it is frequently buried except for its eyes. No change was noted in the overt behavior of this fish between day and night.

Eight specimens (223: 137-277 mm) were speared at various times of the day. Both individuals collected within an hour after sunrise were empty, whereas of six taken during afternoons, two were empty and four contained well-digested fish remains that appeared to have been in the stomachs at least several hours when collected.

Hiatt and Strasburg (1960) reported this flounder on both rocks and sand in the Marshall Islands and noted a diet comprised primarily of fishes that live in sandy areas adjacent to coral. Most prey species listed by them are fishes (balistids, labrids, pomacentrids, and blennies) that probably are active in exposed positions only during daylight. They believed that *B. mancus* responds only to moving prey; if so, at least most of its prey, which rests at night, would not be available after dark. The prey listed by Hiatt and Strasburg also included two species of apogonids, members of what seems to be a universally nocturnal group; however, during daylight these particular apogonid species congregate in exposed positions close among the coral, where they would seem available to diurnal predators.

CONCLUSION.—*Bothus mancus* preys on small fishes during the day. Its nocturnal habits remain uncertain.

General Remarks on Left-hand Flounders

Bothids are the most numerous flatfishes on tropical reefs. In the West Indies, Randall (1967) found fishes the major prey of *Bothus lunulatus* and *B. ocellatus*, both of which occur on sand patches around coral reefs, often largely buried. In the Florida Keys, Starck and Davis (1966) found *B. ocellatus* in sandy areas of all reef zones, and although they did not examine its food habits, they inferred from its behavior that it preys after dark on the various small nocturnal invertebrates active on the sand at night.

ORDER TETRAODONTIFORMES

Family Balistidae: triggerfishes

Melichthys niger (Bloch)—*humuhumu 'ele'ele*

During the day, *M. niger* typically hovers in loosely spaced aggregations several meters above the reef. Each individual independently picks material drifting in the mid-waters. It is a wary animal that dives to holes in the reef when alarmed. It enters these same holes at nightfall and rests there on its side until morning.

All seven individuals (165: 122-195 mm) speared from among those active above the reef during the day were full of food, as listed in Table 63. The major food items are fragments of fleshy algae—filamentous and foliaceous—probably most of which are drifting in the mid-waters when taken. This triggerfish feeds at least occasionally on the sea floor, as indicated by the relatively high

TABLE 63.—Food of *Melichthys niger*.

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Fleshy algae	7	52.3	52.30
2	Coralline algae	7	18.7	18.70
3	Calanoid copepods	5	2.7	1.93
4	Caridean shrimps	4	1.1	0.63
5	Harpacticoid copepods	4	0.6	0.34
6	Scleractinian coral	1	2.1	0.30
7	Insects	2	0.4	0.11
8	Foraminiferans	2	0.3	0.09
9	Heteropods	2	0.3	0.09
10	Cyclopoid copepods	1	0.6	0.09
11	Crab megalops	1	0.4	0.06
12	Mollusk veligers	1	0.1	0.01
13	Naticid gastropods	1	0.1	0.01
14	Ostracods	1	0.1	0.01
15	Gammaridean amphipods	1	0.1	0.01
16	Fish eggs, planktonic	1	0.1	0.01
Also, sand		1	2.9	0.41
	Unidentified fragments	6	17.1	14.66

proportion of coralline algae in its diet and also by the stony coral, bitten off in chunks, in one individual; nevertheless, most of its food is planktonic. Certainly the relatively minor status of the many zooplankters in the above list far understates their relative significance to this fish. The ranking is biased toward the more bulky items; thus, one algal fragment, in terms of volume, may be equivalent to a hundred or more copepods. And yet the effort expended in taking the algal fragment may have been no greater than that expended in taking a single copepod. A given volume of copepods (and many other zooplankters) probably is far more nutritious than the same volume of algae.

In the West Indies, this circumtropical triggerfish similarly feeds on algae and zooplankton in the mid-waters, taking the algae from the benthos, or as drifting fragments (Randall, 1967).

CONCLUSION.—*Melichthys niger* is a diurnal omnivore that feeds mostly on drifting algal fragments and zooplankton, along with some benthic vegetation.

Xanthichthys ringens (Linnaeus)

This triggerfish (Figure 40) is one of the most numerous fishes at depths below 25 m along the outer drop-off. Like so many fishes that concentrate in this location, it aggregates in the water column and picks plankton, an activity that is limited to daylight; at nightfall, it shelters in reef crevices, where it rests on its side until morning.

Of the 11 specimens (125: 98-145 mm) speared during day and night, 2 that were collected from reef crevices during the last hour before daybreak were empty, whereas all 9 that were taken from mid-water aggregations at various times during the day were full of food, as listed in Table 64.

I found no evidence that this triggerfish takes food from the sea floor. Like *Melichthys niger*, *X. ringens* is circumtropical (Böhlke and Chaplin, 1968); perhaps the planktivorous habits of these two triggerfishes permit survival over long periods in the open sea where their bottom-feeding relatives would perish. Gosline and Brock (1960), whose data were mostly from relatively shallow water, reported *X. ringens* uncommon in Hawaii. The large numbers of this species occurring along the outer drop-off in Kona, however, indicates a habitat in Hawaii similar to that in the West Indies, where it rarely occurs in less than 35 m of water, but is one of the most numerous fishes below that depth (Randall, 1968).

CONCLUSION.—*Xanthichthys ringens* is a diurnal planktivore that feeds mostly on calanoid copepods.

Rhinecanthus rectangulus (Bloch and Schneider)—*humuhumu nukunuku a pua'a*

This triggerfish is most common on shallow, surge-swept, basalt reefs. It is a solitary fish that swims close to the reef top during the day, picking at organisms on the bottom. A wary animal, it quickly takes refuge in the reef when threatened.

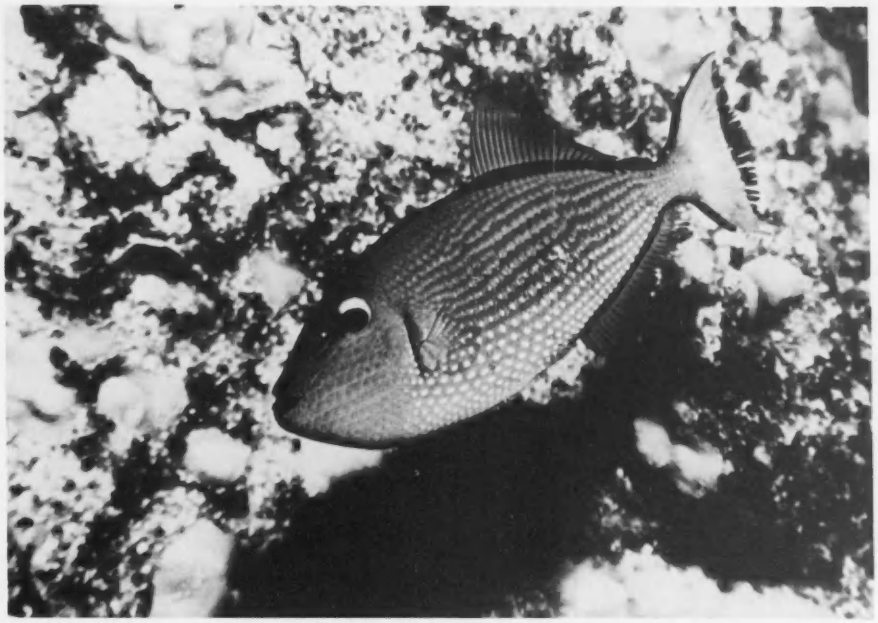

FIGURE 40.—*Xanthichthys ringens*, a zooplanktivorous triggerfish. In comparison with bottom-feeding triggerfishes, this species has a more upturned mouth that is higher on its head, and its body is more fusiform. Both features are widespread among zooplanktivorous fishes.

Its shelters, like those of *Melichthys niger*, above, are small enough so that the fish can wedge itself in by locking its large dorsal spine erect. Each individual fish seems to resort to a specific hole that serves as a refuge by day, and also as a resting place at night when the species is inactive.

All nine individuals (142: 114-170 mm) speared at various times of the day from among those active close to the reef were full of food, as listed in Table 65. Food items were mostly small organisms between 1 and 6 mm in their greatest dimension, taken intact; the few exceptions are fragments of about this size from larger organisms.

Hiatt and Strasburg (1960) found this species numerous on shallow reefs in the Marshall Islands and reported a crustacean and algal diet similar to that of the species in Kona.

TABLE 64.—Food of *Xanthichthys ringens*.

Rank	Items	No. fish with this item (n = 9)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	9	43.9	43.90
2	Mollusk veligers	6	0.8	0.53
3	Fish eggs, planktonic	2	1.4	0.31
4	Chaetognaths	2	1.3	0.29
5	Siphonophores	2	1.2	0.27
6	Pteropods	2	1.2	0.27
7	Ostracods	4	0.6	0.27
8	Cyclopoid copepods	1	0.8	0.09
9	Heteropods	2	0.3	0.07
10	Hyperiid amphipods	2	0.2	0.04
11	Gammaridean amphipods	1	0.2	0.02
Also, crustacean fragments		4	4.6	2.04
	Unidentified fragments	9	43.5	43.50

TABLE 65.—Food of *Rhinecanthus rectangulus*.

Rank	Items	No. fish with this item (n = 9)	Mean percent of diet volume	Ranking index
1	Gammaridean amphipods	9	19.4	19.40
2	Didemnid tunicates	9	8.6	8.60
3	Filamentous algae	6	7.8	5.20
4	Xanthid crabs	4	6.7	2.98
5	Polychaetes	4	6.3	2.80
6	Decapod shrimps	5	4.2	2.33
7	Tanaids	4	2.9	1.29
8	Coralline algae	4	2.6	1.16
9	Prosobranch gastropods	4	2.4	1.07
10	Echinoids	3	2.9	0.97
11	Isopods	3	2.6	0.87
12	Bryozoans	2	0.7	0.16
13	Caprellid amphipods	1	0.6	0.07
14	Pelecypods	1	0.3	0.03
15	Crab megalops	1	0.2	0.02
Also, crustacean fragments		4	6.2	2.76
	Unidentified fragments	7	25.6	19.91

TABLE 66.—Food of *Sufflamen bursa*.

Rank	Items	No. fish with this item (n = 9)	Mean percent of diet volume	Ranking index
1	Echinoids	9	9.1	9.10
2	Gammaridean amphipods	7	8.3	6.46
3	Polychaetes	8	4.6	4.09
4	Prosobranch gastropods	9	3.8	3.80
5	Brachyurans	5	4.8	2.67
6	Sponges	8	2.6	2.31
7	Tanaids	6	2.8	1.87
8	Opisthobranchs	6	2.3	1.53
9	Cyclopoid copepods	9	1.2	1.20
10	Isopods	7	1.3	1.01
11	Ostreid pelecypods	7	1.0	0.78
12	Caridean shrimps	3	0.8	0.27
13	Foraminiferans	4	0.4	0.18
14	Ostracods	4	0.4	0.18
15	Crab megalops	2	0.3	0.07
16	Bryozoans	1	0.1	0.01
17	Sipunculid introverts	1	0.1	0.01
18	Harpacticoid copepods	1	0.1	0.01
19	Barnacle cirri	1	0.1	0.01
20	Mites	1	0.1	0.01
Also, crustacean fragments		5	3.8	2.11
	Algal fragments	5	1.2	0.67
	Unidentified fragments	9	50.8	50.80

CONCLUSION.—*Rhinecanthus rectangulus* is a diurnal omnivore, feeding mostly on gammaridean amphipods and other small organisms.

Sufflamen bursa (Bloch and Schneider)—*humuhumu umauma lei*

This is the most numerous and widespread triggerfish on Kona reefs. A solitary species, active by day close to rocks and coral, it picks at organisms on the sea floor. It is less inclined to seek cover in reef crevices than are *Melichthys niger* and *Rhinecanthus rectangulus*, above, but nevertheless is a wary animal that shys away from humans. At night it is inactive, resting on its side under cover on the reef until morning.

Thirteen individuals (140: 109-164 mm) were speared at various times of day and night. The four that were collected in darkness as they rested in reef crevices during the last 2 h before daybreak were empty, whereas the nine that were collected at various times during the day as they swam over the reef were full of food, as listed in Table 66. As was true of the food of *R. rectangulus*, these food items, including the echinoids, are mostly small animals between 1 and 6 mm in their greatest dimension, taken intact; the exceptions are fragments of about this size from larger organisms. Unlike the omnivorous *R. rectangulus*, however, *S. bursa* seems to be strictly carnivorous (the few algal fragments among its gut contents probably were taken incidentally along with prey). No

single item greatly predominates in its diet, a circumstance that may relate to its widespread occurrence in a variety of habitats.

CONCLUSION.—*Sufflamen bursa* is a diurnal predator that feeds on a variety of benthic animals.

General Remarks on Triggerfishes

The balistids are known for their powerful jaws and sharp cutting teeth, which enable them to prey on a variety of armored invertebrates denied as food to most other fishes (Randall, 1967). Most triggerfishes seem to make full use of this equipment: in the Virgin Islands *Balistes vetula* preys on the large echinoid *Diadema* (often attacking this sea urchin from its oral surface, where the spines are shortest) and on relatively large queen conchs, *Strombus*, which it crushes upon ingestion (Randall, 1967). Similarly, in the Marshall Islands several triggerfishes use their powerful feeding apparatus to crush mollusks and hard-shelled crustaceans, as well as to break off the tips of cespitose corals (Hiatt and Strasburg, 1960). *Rhinecanthus rectangulus* and *Sufflamen bursa* in Kona may be exceptional among bottom-foraging balistids in that they feed so heavily on small organisms, ingested intact. On the other hand, it may be that the high proportion of unidentified fragments in the guts of both species are the crushed remains of larger organisms not properly ranked among the data. Nevertheless, the capacity to feed on tiny organisms is probably well established among the balistids, as demonstrated by the exclusively zooplanktivorous habits of *Xanthichthys ringens*.

Triggerfishes are well known to be active by day and to rest under cover at night, usually lying on their sides. Diurnal habits were reported in balistids of the Gulf of California (Hobson, 1965, 1968a) and the West Indies (Randall, 1967). Collette and Talbot (1972) described *Balistes vetula* sleeping at night in exposed positions on reefs in the Virgin Islands, and Earle (1972) reported that in the Virgin Islands *B. vetula* frequently returns nightly to the same hole in the reef. There is at least some activity among triggerfishes on moonlit nights, however, as for example in *B. polylepis* in the Gulf of California (Hobson, 1965), but it is unknown whether this activity involves feeding.

Family Monacanthidae: filefishes

Cantherines dumerili (Hollard)—*'o'ili*

During daylight, this filefish swims several meters above coral-rich reefs, usually in loosely associated pairs that move, often on their sides, back and forth in restricted, well-defined areas. Because it swims in the water column and because it is relatively large, this filefish is a conspicuous component of the fauna, even though relatively few occur on the reef. Despite the time it spends in mid-water, *C. dumerili* was observed feeding only on the sea floor, where it bites off the tips of coral branches. During evening twilight it settles into holes in the reef, where it remains inactive until morning.

All eight individuals (200: 171-240 mm) speared from among those hovering above the reef during midday were full of food. Scleractinian corals were the major food items, occurring in seven of the eight specimens (mean percent of diet volume: 80; ranking index: 70), always as chunks of *Pocillopora* and *Porites*, about 4 mm in diameter. Other food items were: echinoids, all tips of the clublike spines of *Heterocentrotus mammillatus*, in two (mean percent of diet volume: 7.4; ranking index: 1.85), a variety of bryozoans, both encrusting and arborescent, that were almost the total contents of one (mean percent of diet volume: 12.5; ranking index volume: 1.56), and pelecypods in one (mean percent of diet volume: 0.1; ranking index: 0.01).

Hiatt and Strasburg (1960) found that of the two specimens of this species (reported as *Amanses carolae)* that they examined in the Marshall Islands, one had fed on scleractinian corals exclusively, whereas the other had mixed a coral diet with sponges and algae. Apparently this species does not feed during the considerable time that it spends in the water column, as its diet seems to comprise only benthic organisms.

CONCLUSION.—*Cantherines dumerili* is a diurnal predator that feeds mainly on scleractinian corals.

Cantherines sandwichiensis (Quoy and Gaimard)—*'o'ili lepa*

This, the most numerous filefish in Kona, especially on basalt reefs in less than 10 m of water, is a solitary fish that swims close over the reef during

TABLE 67.—Food of *Cantherines sandwichiensis*.

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Filamentous algae	7	35.7	35.70
2	Coralline algae	7	32.1	32.10
3	Didemnid tunicates	7	6.1	6.10
4	Gammaridean amphipods	6	4.0	3.43
5	Scleractinian corals	2	5.0	1.43
6	Sponges	2	2.2	0.63
7	Diatoms	3	1.1	0.47
8	Bryozoans	2	1.0	0.29
9	Hydroids	2	0.4	0.11
10	Polychaetes	1	1.4	0.20
11	Ostreid pelecypods	2	0.6	0.17
12	Caprellid amphipods	2	0.6	0.17
13	Gastropod eggs	1	0.3	0.04
14	Prosobranch gastropods	1	0.3	0.04
15	Tanaids	1	0.1	0.01
16	Ophiuroids	1	0.1	0.01
Also, unidentified fragments		5	8.3	5.93
	Sand	1	0.7	0.10

TABLE 68.—Food of *Pervagor spilosoma*.

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Scleractinian corals	5	35.8	29.83
2	Filamentous algae	4	19.3	12.87
3	Coralline algae	6	7.7	7.70
4	Sponges	1	3.3	0.55
5	Polychaetes	2	1.5	0.50
6	Echinoids	3	0.8	0.40
7	Gammaridean amphipods	3	0.7	0.35
8	Tanaids	2	0.5	0.16
9	Diatoms	2	0.3	0.10
10	Fish eggs	1	0.5	0.08
11	Hydroids	2	0.3	0.10
12	Opisthobranch gastropods	1	0.2	0.03
13	Ostracods	1	0.2	0.03
14	Cyclopoid copepods	1	0.2	0.03
15	Crab megalops	1	0.2	0.03
16	Ophiuroids	1	0.2	0.03
Also, unidentified fragments		5	28.1	23.41
	Sand	1	0.2	0.03

the day, picking at objects on the bottom. During evening twilight, it moves from sight and is not visible at night when presumably it rests in reef crevices.

All seven individuals (116: 84-132 mm) speared from among those active close to the reef during the day were full of food, much of it fresh, as listed in Table 67.

CONCLUSION.—*Cantherines sandwichiensis* is a diurnal omnivore that feeds on a wide variety of benthic algae and invertebrates.

Pervagor spilosoma (Lay and Bennett)—*'o'ili 'uwi'uwi*

This, the most colorful filefish in Kona, as well as the smallest of the three considered there, is most numerous on coral-rich reefs. It is a solitary fish, active close among the corals in daylight, but not seen after dark when presumably it rests in reef crevices.

Of the seven specimens (85: 64-120 mm) collected, one that was speared close to coral just before sunrise (the first individual of the species to appear that morning) had an empty gut, whereas all six that were speared from among those active on the reef between midmorning and midafternoon were full of food, as listed in Table 68.

As is true of *Cantherines dumerili*, above, the major food of this filefish is scleractinian coral; however, whereas *C. dumerili* bites off relatively large chunks of coral, each containing many polyps, *P. spilosoma* seems to pluck at only one polyp at a time, as do certain chaetodontids. Nevertheless, judging from its gut load of skeletal

fragments, *P. spilosoma* does not neatly snip off the polyps so much as coarsely gouge them from their thecae.

CONCLUSION.—*Pervagor spilosoma* is a diurnal omnivore that feeds mainly on scleractinian corals, to a lesser extent on algae and other benthic invertebrates.

General Remarks on Filefishes

In summarizing their treatment of monacanthids in the Marshall Islands, Hiatt and Strasburg (1960:105) stated: "There is no question that filefishes derive the bulk of their nutriment from living corals." All of the *Oxymonocanthus longirostris* (a widespread Indo-Pacific species that does not occur in Hawaii) examined by them contained only coral polyps, with no skeletal material. Their account indicates that this species, which has a very long, narrow snout, with teeth protruding from its mouth as long, cupshaped incisors, may be among the most highly specialized of coral-feeding filefishes. On the other hand, Randall (1967) found corals to be insignificant as food for West Indian filefishes; of the six species he examined, corals were in the diet of only one, and only as a minor component. According to Randall, the West Indian filefishes take a diverse array of benthic organisms: Algae and sea grasses are major items, along with a variety of benthic invertebrates. Thus, *Cantherines sandwichiensis* in Kona has a diet much like the West Indian species described by Randall, whereas *C. dumerili* takes largely corals in Kona, just as Hiatt and Strasburg reported it and other filefishes doing in the Marshall Islands. Clearly, many filefishes, especially certain Indo-Pacific species, feed heavily on corals, whereas various other filefishes find their food from among other elements of the benthos.

Filefishes are recognized as being diurnal. For example, Starck and Davis (1966) described *C. pullus* as resting at night wedged in rocky holes on reefs in Florida.

Family Ostraciontidae: boxfishes

Ostracion meleagris (Shaw)—*pahu*

This boxfish is widespread on nearshore reefs in Kona, but is nowhere numerous, except occasionally in some parts of the boulder habitat. During the day it swims, slowly, close among rocks and coral, now and then picking at the substratum. I saw several in the same places at night, but at the time felt they had been disturbed from resting places by my activity. It was difficult to appraise the nocturnal behavior of this species, owing to its relatively low numbers on the reef and the reduced visibility after dark, and because the few observations were somewhat ambiguous.

Of the six individuals (65: 43-80 mm) collected, one speared within 15 min after sunrise as it swam close to the reef had an empty gut, whereas all five taken under similar circumstances, except later in the day (between late morning and late afternoon) had food throughout the gut. The items in the foregut are listed in Table 69.

CONCLUSION.—*Ostracion meleagris* feeds on benthic invertebrates during the day. Its nocturnal status remains uncertain, although tenuous data indicate relative inactivity after dark.

General Remarks on Boxfishes

Boxfishes in the tropical Atlantic generally are described as active during both day and night (Starck and Davis, 1966; Earle, 1972; Collette and Talbot, 1972). Tunicates, the major prey of *Ostracion meleagris* in Kona, were ranked either

TABLE 69.—Food of *Ostracion meleagris*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Didemnid tunicates	3	42.8	25.68
2	Polychaetes	2	13.0	5.20
3	Algae	2	7.4	2.96
4	Sponges	1	2.0	0.40
5	Pelecypods	1	1.0	0.20
6	Prosobranch gastropods	1	1.0	0.20
7	Copepods	1	0.4	0.08
Also, sand and debris		1	6.0	1.20
	Unidentified fragments	2	26.4	10.56

first or second as prey of three of the five West Indian boxfishes studied by Randall (1967). Furthermore, polychaetes and sponges also were found to be important prey in the Atlantic species just as they are in *O. meleagris* from Kona. In the Marshall Islands, the major foods of *O. cubicus* are mollusks, polychaetes, and algae (Hiatt and Strasburg, 1960).

At least some boxfishes, including *O. meleagris* in Hawaii (Gosline and Brock, 1960; Thomson, 1964), release a substance that is toxic to other fishes. This may give them some immunity from predation, as suggested for some tropical Atlantic species by Randall (1967).

Family Tetraodontidae: balloonfishes

Arothron hispidus (Linnaeus)—*'opu hue, keke*

This solitary balloonfish is widespread on Kona reefs, but is nowhere numerous. In daylight it frequently hovers inactively several meters above the reef, although just as often it swims slowly among the rocks and coral. After dark it continues to swim actively, close to the reef.

Nine individuals (253: 187-332 mm) were speared during day and night. The guts of two were empty: one of these was hovering high in the water column during early afternoon when collected; the other was swimming close among rocks during the hour immediately before first morning light. All of the other seven, taken as they swam close to the reef—five during midday, two during midnight—contained identifiable material, as listed in Table 70. The tunicates taken by this balloonfish include several benthic species, both compound and simple forms; the echinoids are the crushed tests and spines of echinometrids and cidarids; the asteroids are mostly tips of the appendages from *Linckia*.

Generally the items are hard-bodied forms that remain recognizable for a relatively long time after ingestion; nevertheless, material from the two individuals collected at night appeared fresher overall than that from the individuals collected during midday.

In the Marshall Islands, the single *A. hispidus* examined by Hiatt and Strasburg (1960) had fed on much the same material as listed above, except that it also had ingested some living scleractinian corals.

CONCLUSION.—*Arothron hispidus* preys on a variety of benthic invertebrates, especially those having a hard or leathery external covering. Limited evidence indicates it is active during both day and night.

Arothron meleagris (Bloch and Schneider)—*'opu hue, keke*

Like its congener *A. hispidus*, above, the solitary species *A. meleagris* (Figure 41) is widespread on Kona reefs, but is nowhere numerous. It does not hover inactively above the reef during the day as *A. hispidus* often does, and on the few occasions when it was seen at night—always under ledges or in crevices—*A. meleagris* seemed inactive. During daylight it swims slowly among the rocks or corals.

Eleven individuals (221: 146-393 mm) were collected during the day. Of three whose guts were empty, two were speared as they swam close to the reef within an hour after sunrise, and one was taken from a small cave during midafternoon. The remaining eight, taken as they swam close to the reef during midday, all contained identifiable material. Seven of these had taken scleratinian corals (mean percent of diet volume: 43.1; ranking index: 37.71), mostly small chunks of encrusting

TABLE 70.—Food of *Arothron hispidus*.

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Tunicates	5	33.7	24.07
2	Echinoids	5	28.1	20.07
3	Ophiuroids	3	13.4	5.74
4	Asteroids	3	8.3	3.56
5	Brachyurans	2	6.4	1.83
6	Sponges	1	2.9	0.41
7	Hydroids	1	2.9	0.41
8	Prosobranch gastropods	1	0.1	0.01
9	Pagurid crabs	1	0.1	0.01
Also, algae		1	0.3	0.04
	Unidentifiable fragments	3	3.8	1.63

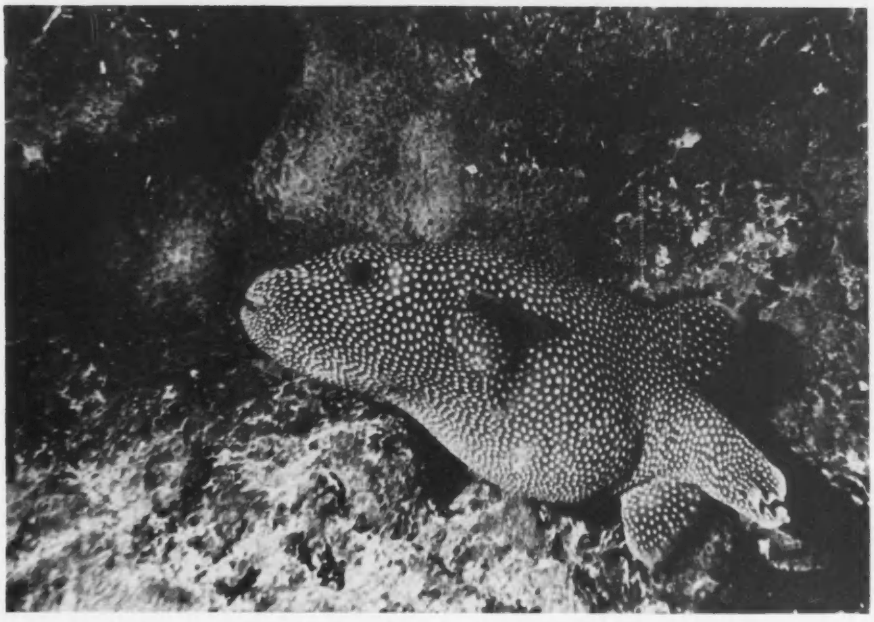

FIGURE 41.—*Arothron meleagris*, a balloonfish. By inflating its saclike body with water, this slow-swimming fish increases its size, which presumably decreases its vulnerability to predators.

Porites, whereas six had taken tunicates (mean percent of diet volume: 44.4; ranking index: 33.3), all of them a large colonial form with a heavy black integument that, like the coral, encrusts on rocks. The only other recognizable items were pectinid pelecypods in one (mean percent of diet volume: 0.6; ranking index: 0.08). Three contained unidentifiable fragments (mean percent of diet volume: 11.9; ranking index: 4.46). Thus, these data indicate that, compared with *A. hispidus*, *A. meleagris* is a relatively specialized feeder. The three *A. meleagris* that Hiatt and Strasburg (1960) examined in the Marshall Islands had fed almost exclusively on living corals.

CONCLUSION.—*Arothron meleagris* is a diurnal predator that feeds mostly on corals and tunicates which encrust on rocks.

General Remarks on Balloonfishes

The dentition of tetraodontids consists of heavy plates, two in each jaw, that form a sharp beak. With this exceptionally strong apparatus, these fishes crush an array of armored organisms that are unavailable as prey to most other fishes (Hiatt and Strasburg, 1960).

Family Canthigasteridae: sharpbacked puffers

Canthigaster amboinensis Bleeker — *pu'u ola'i*

This pufferfish occurs chiefly in relatively shallow water where there is much exposed basalt. It is a solitary fish, active close to the sea floor during the day, but only infrequently in view after dark, when, presumably, it generally retires to reef crevices.

All 11 individuals (69: 31-91 mm) that were speared at various times during daylight contained identifiable material (much of it fresh), as listed in Table 71.

CONCLUSION.—*Canthigaster amboinensis* is a diurnal omnivore that feeds mostly on coralline algae and various hard-bodied invertebrates.

TABLE 71.—Food of *Canthigaster amboinensis*.

Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Coralline algae	10	42.5	38.64
2	Filamentous algae	8	9.4	6.84
3	Scleractinian corals	6	7.7	4.20
4	Pectinid pelecypods	2	7.8	1.42
5	Brachyurans	2	7.3	1.33
6	Ophiuroids	2	4.9	0.89
7	Echinoids	4	2.4	0.87
8	Sponges	5	1.3	0.59
9	Prosobranch gastropods	4	0.6	0.22
10	Bryozoans	2	0.6	0.11
11	Sipunculid introverts	2	0.3	0.05
12	Foraminiferans	3	0.2	0.05
13	Gammaridean amphipods	2	0.2	0.04
14	Didemnid tunicates	1	0.3	0.03
15	Polychaetes	1	0.2	0.02
Also, unidentified fragments		6	14.3	7.80

TABLE 72.—Food of *Canthigaster jactator*.

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Coralline algae	3	15.7	7.85
2	Prosobranch gastropods	4	11.2	7.47
3	Sponges	3	6.8	3.40
4	Scleractinian corals	2	10.0	3.33
5	Filamentous algae	5	3.7	3.08
6	Didemnid tunicates	3	6.0	3.00
7	Sipunculid introverts	3	4.3	2.15
8	Echinoids	2	5.5	1.83
9	Bryozoans	2	1.3	0.43
10	Brachyurans	2	1.3	0.43
11	Diatoms	3	0.7	0.35
12	Foraminiferans	2	0.3	0.10
13	Ophiuroids	1	0.3	0.05
14	Ostracods	1	0.2	0.03
15	Gammaridean amphipods	1	0.2	0.03
16	Isopods	1	0.2	0.03
17	Caridean shrimps	1	0.2	0.03
Also, crustacean fragments		1	5.0	0.83
	Sand	3	1.5	0.75
	Unidentified fragments	5	25.6	21.33

Canthigaster jactator (Jenkins)

This small pufferfish lives mostly where corals are well developed. Like its congener *C. amboinensis*, above, it is mostly solitary, although sometimes several occur together. It swims close among the coral during daylight, but is only occasionally in view at night, probably because it usually rests in reef crevices after dark. Once during the predawn hours, as noted above, I observed a nocturnally active moray eel, *Gymnothorax petelli*, grasping one of these puffers between its jaws.

Thirteen individuals (50: 40-70 mm) were speared at various times of day and night. Four were taken during daylight, and these were the only ones that had material in the anterior third of their gut, much of it relatively fresh. In two others taken at night (one 4 h after sunset, the other during the last hour before daybreak), food was confined to the posterior two-thirds of their guts, but much of it was still largely identifiable. In comparison, the remaining seven, collected either at night (more than 4 h after sunset), or during morning twilight, were empty. Items in the six specimens that contained identifiable material are listed in Table 72.

CONCLUSION.—*Canthigaster jactator* is a diurnal omnivore that feeds mostly on coralline algae and various hard-bodied benthic invertebrates.

Remarks on Sharpbacked Puffers

The canthigasterids are widely recognized as omnivorous fishes that feed on benthic plants and

invertebrates (e.g. in the tropical Atlantic by Randall, 1967; and in the western Pacific by Hiatt and Strasburg, 1960). Most investigators have considered them diurnal. Smith and Tyler (1972) described *Canthigaster rostratus* sleeping at night on reefs in the Virgin Islands; Collette and Talbot (1972) also suspected *C. rostratus* to be nocturnally inactive, and suggested that some they saw swimming at night had been disturbed by their lights. To Starck and Davis (1966), however, at least some individuals of *C. rostratus* appeared to be nocturnally active in the Florida Keys; however, they recognized that this species is active in daylight as well.

Family Diodontidae: spiny puffers

Diodon holocanthus Linnaeus — *kokala*

This spiny puffer is numerous in Kona, where it frequently swims close above the reef at night; nevertheless, I never saw one there in daylight. Undoubtedly, it is under shelter during the day, probably deep within the coral caverns that honeycomb much of the reef. In the Gulf of California, where the rocky sea floor offers mostly ledges and relatively shallow caves, one often sees the nocturnally active *D. holocanthus* resting in these places during the day.

All five individuals (211: 175-239 mm) that were speared as they swam in exposed locations on the reef after dark contained identifiable material in their guts, much of it relatively fresh. Prosobranch gastropods, which occurred in all five specimens, were the major food item (mean percent of diet volume and ranking index: 54.1), with pagurid crabs also important prey of all five (mean percent of diet volume and ranking index: 24). Other food items were: echinoids, all *Echinometra mathaei*, in four (mean percent of diet volume: 18; ranking index: 14.4), and ophiuroids in two (mean percent of diet volume: 3.9; ranking index: 1.56). Although this material had been crushed by the powerful jaws and beaklike dentition of the fish, it was apparent that at least many of the gastropod shells actually had housed pagurid crabs; thus the pagurids, not the gastropods themselves, may have been the major food. It remains uncertain how many living gastropods are in fact taken, although opercula among the gut contents showed that living gastropods are important prey.

This circumtropical species has a similar diet in the Atlantic Ocean, as determined by Randall (1967), who also listed prosobranch gastropods as the major food item. He listed pagurid crabs too, but did not suggest that some of the gastropods on his list may have been shells that housed these crabs.

Diodon holocanthus is nocturnal in the Florida Keys, where it stays under ledges or in holes during the day, but emerges at night to feed on various invertebrates, particularly larger shelled forms (Starck and Davis, 1966).

CONCLUSION.—*Diodon holocanthus* is a nocturnal predator that feeds mostly on prosobranch gastropods and pagurid crabs.

Diodon hystrix Linnaeus—*kokala*

During the day, *D. hystrix* either is secreted under ledges, or hovers inactively high in the water column, often several together. At night, solitary individuals (Figure 42) swim in exposed locations close above the reef, especially among basaltic boulders.

Of the 16 individuals (263: 244-333 mm) speared during day and night, only 4 had empty guts, and these were collected during late afternoon, either from holes under rocks, or as they hovered in the water column. The only ones that carried food in the anterior third of their gut were taken at night—two during the hour before midnight and one 2 h before daybreak. Although the anterior third of the gut was empty in the other nine, all carried material posteriorly, which, composing entirely shelled organisms, was readily identifiable: two of these specimens were collected at night—one at midnight, the other just before daybreak; the remaining seven were taken during the day—four of them in the morning, three early in the afternoon. In all, 12 specimens contained identifiable prey.

Echinoids, including both cidarids and echinometrids, occurred in 11 of the 12 specimens and were the major food item (mean percent of diet volume: 55; ranking index: 50.42). Prosobranch gastropods, present in 11 (mean percent of diet volume: 27.1; ranking index: 24.84), were ranked second, and pagurid crabs, also present in 11 (mean percent of diet volume: 12.9; ranking index: 11.83), were ranked third. Thus, the diet includes items similar to those taken by *D. holocanthus*, above, but ranked in a different order. As is true of the material from *D. holocanthus*, many of the gastropod shells had housed pagurid crabs, but the

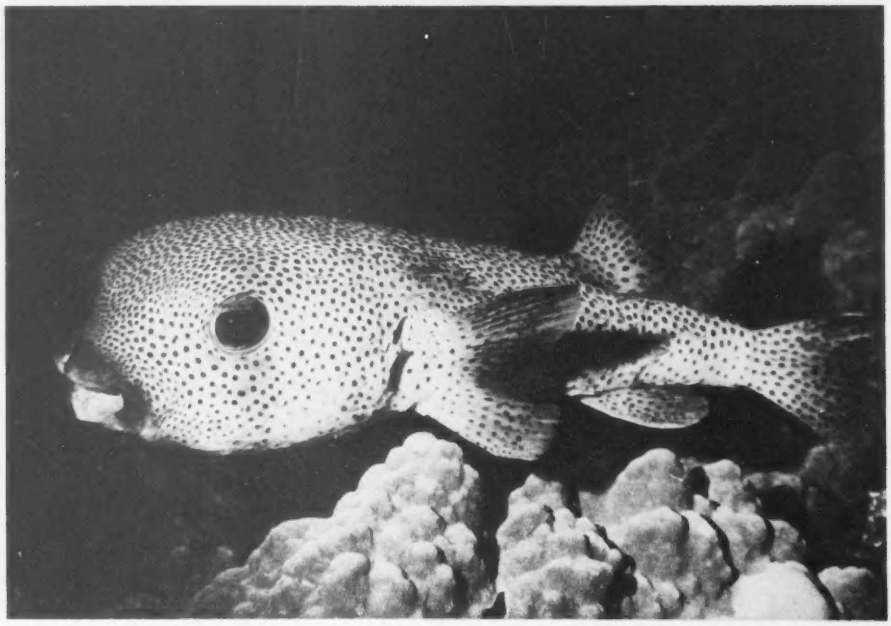

FIGURE 42.—*Diodon hystrix*, a spiny puffer, swimming above the reef at night. With its heavy, beaklike dentition, this fish crushes its shelled prey.

number remains unknown. Nevertheless, the pagurids may actually rank second as prey even though the opercula among this material show that living gastropods are important prey. One *D. hystrix* also contained ostreid pelecypods (mean percent of diet volume: 0.8; ranking index: 0.07), and one contained unidentified fragments (mean percent of diet volume: 4.2; ranking index: 0.35).

Randall (1967) similarly found echinoids the major food of this circumtropical species in the West Indies. For this species as well as *D. holocanthus*, Randall listed gastropods and pagurids separately, without suggesting that some of the gastropods may have been only shells which housed pagurids. Randall recognized that *D. hystrix* feeds partly by night, but believed it to be primarily diurnal. Starck and Davis (1966), however, reported strictly nocturnal habits for *D. hystrix* in the Florida Keys.

The strong, sharp spines that cover *D. hystrix* and *D. holocanthus* are perhaps their most distinctive morphological characteristic. These spines lie flat against their bodies most of the time, but when the bodies inflate with water—a regular response to threats—the spines stand straight out. Although this formidable defense probably deters most predators, the slow-moving *Diodon* would be ready prey for those predators able to tolerate the spines and inflated body. In Hawaii, the tiger shark, *Galeocerdo cuvieri*, regularly preys on full-grown adults of *D. hystrix* (Tester, 1963).

CONCLUSION.—*Diodon hystrix* is a nocturnal predator that feeds mostly on echinoids, and to a lesser extent on prosobranch gastropods and pagurid crabs.

General Remarks on Spiny Puffers

The teeth in both upper and lower jaws of the diodontids are fused together to produce a solid, heavy beak, and this apparatus enables them to crush some of the larger, heavily shelled prey that are beyond the capacity of other fishes—even their relatives the balloonfishes.

The nocturnal habits of the two species of *Diodon*, described above, may be a family characteristic. Starck and Davis (1966) reported that two species of *Chilomycterus* in Florida—*antillarum* and *schoepfi*—are active at night and inactive during the day.

DISCUSSION

The habits of fishes on Kona reefs exemplify the habits of fishes on coral reefs around the world. The following discussion relates these habits to the evolution of fishes on modern tropical reefs, stressing the selective pressures that have shaped the diverse array of forms coexisting on these reefs today. I refer to some of these forms as more advanced, or specialized than others, even though all are products of an equally long evolution, and each is well adaptated to its own specific way of life. Some, nevertheless, have diverged more than others from the generalized carnivores that gave rise to them all, and in this fact lies the basis for the discussion.

The categories erected for presentation have indistinct, overlapping limits, and some species are discussed under one category, rather than another, quite arbitrarily. Nevertheless, the synthesis presented, though an oversimplification, provides a frame of reference within which new information may be assessed. Reemphasizing a point made above, this report deals only with individuals of the various species that behave as adults.

Coral Reefs as a Habitat for Fishes

Most fishes that inhabit coral reefs are among the more recently evolved teleosts (Schaeffer and Rosen, 1961; and others). Indeed, much of the diversity among higher teleosts expresses adaptations to reef habitats. Of the fishes observed along Kona transect lines (Table 7), 98.5% are acanthopterygians.[8]

To properly appreciate the relation of modern coral-reef fishes to their habitat, one should be familiar with the history of tropical reefs. The following outline is based on Newell (1971).

The evolution of tropical reefs can be traced through a fossil record that reaches back into the Precambrian. By the Mid-Ordovician, over 400 million years ago, animal communities had become associated with coral-algal reefs. A succession of reef communities then evolved during subsequent geological history, each with its own characteristic assemblage of animals, and each achieved marked stability before crashing into oblivion during worldwide environmental upheavals. Between each of these periods of stable reef communities, a long time passed without known reefs.

The scleractinian corals, which dominate modern reefs, first appeared during the Triassic, and by Jurassic times, about 150 million years ago, the lithothamnion-scleractinian reef community was well established. Significantly, the teleostean radiation also began during the Jurassic (Gosline, 1971), indicating that their history may closely interrelate with that of the lithothamnion-scleractinian reef community. But Smith and Tyler (1972) suggested that the preacanthopterygian teleosts and their forebearers were maladapted to reef conditions. They contended that fishes entered reef habitats only upon acquiring certain of the morphological advances that marked the first appearance of acanthopterygians early during the Cretaceous, over 100 million years ago. Newell (1971), on the other hand, believed that fishes have had a much longer history as reef inhabitants. He attributed their absence in the fossil record of early reefs to their skeletal remains having been "destroyed by scavengers that abound in this strongly oxidizing environment."

It is unquestioned, nevertheless, that early acanthopterygian fishes—the Beryciformes—were better adapted than were their predecessors for reef habitats. Their increased success probably was based mostly on increased maneuverability and a more adaptive feeding mechanism—the features which Smith and Tyler (1972) felt were especially suited for coral reefs. Patterson (1964) underscored this point when he concluded that most skeletal differences between acanthopterygians and their primitive elopidlike ancestors resulted from changes that permitted the fish better maneuverability: most significant, the fins, given increased rigidity by replacing the anterior soft rays with spines, were more effectively positioned, and the body was shortened and deepened. The advances these fishes made in their feeding mechanism was especially significant, as attested by Schaeffer and Rosen (1961), who stated: "It is primarily the acanthopterygian

[8]Because most of the transect counts were made in daylight, there is a bias toward the more advanced forms in numbers of species (the greater incidence of diurnally secretive habits among the more primitive forms, and of diurnally exposed habits among the more highly evolved forms, is discussed below). Even so, however, the preponderance of acanthopterygians is overwhelming, especially if one also considers numbers of individuals. On Kona reefs such advanced groups as the labrids, pomacentrids, and acanthurids are among the species with the largest numbers of individuals. And although among the nonacanthopterygians the numerous muraenid eels are not properly represented in the counts, neither are such nocturnal acanthopterygians as the numerous holocentrids.

mouth that has given rise to the enormous variety of specialized feeding mechanisms for which teleosts are so well known. Presumably, the evolution of the acanthopterygian jaw mechanism promoted the successful exploitation of food sources that previously were largely unavailable to actinopterygian fishes." They referred to the protrusible premaxillary of acanthopterygians, which permits them to project their upper jaw at food. Fishes with this mouth construction can accommodate the shape and size of the mouth opening more appropriately to the shape of the food item than can fishes without a protusible premaxillary (Alexander, 1967; Gosline, 1971).

During the Cretaceous, in which the beryciforms flourished, the ecological role of the scleractinian corals was challenged by a group of bivalved mollusks, the rudists, which underwent an extraordinary radiation and became the center of a highly successful and widespread reef community. But at the end of the Cretaceous, about 70 million years ago, these and other reef communities collapsed in sweeping extinctions associated with the worldwide biological revolution that marked the close of the Mesozoic (Newell, 1971).

Tertiary seas over most of the world were without known coral-reef communities until lithothamnion-scleractinian reefs underwent a second major radiation during the Eocene, about 50 million years ago (Newell, 1971). The communities that developed in association with these reefs are essentially those of our time. And in what would seem a related phenomenon, the explosive radiation of acanthopterygians into the types that inhabit modern reefs also occurred during the Eocene (Patterson, 1964). Of the families living on reefs today, only a relatively few can be traced back in time earlier than the Eocene (Berg, 1940), and yet by the end of that period, which spanned about 15 million years, representatives of almost every major type of modern fish had appeared (Romer, 1966).

This most recent proliferation of acanthopterygians probably radiated from a line of generalized percoidlike carnivores that had arisen from among the Beryciformes during the late Cretaceous (Gosline, 1966). Above, I note that 98.5% of the fishes seen on Kona transect lines are acanthopterygians; more specifically, 90.4% are acanthopterygians that have reached, or passed, the percoid level of structural development, and 75.5% belong to the order Perciformes (see footnote 7). Only the holocentrids represent the ancestral Beryciformes. In fact, worldwide the Holocentridae, and a few species of Anamalopidae, are the only representatives of this once prolific order that have survived on nearshore reefs.

Obviously the percoid level of development has been highly successful. Gosline (1971) pointed out: "In no single way does it seem to differ from that of the now unimportant, perhaps relic Beryciformes from which it was presumably derived. Possibly the percoids have developed some distinct and as yet unknown biological advantage over the Beryciformes, but for the moment one can only assume that the percoids represent a successful integration of minor advances." The minor advances which Gosline cited include increased maneuverability and adaptability of the protrusible jaw mechanisms, which are refinements on those same features adaptive to reef living that probably gave the Beryciformes an advantage over their progenitors.

Generalized Carnivores: Main Line of Teleostean Evolution

From early Mesozoic times the main line of actinopterygian evolution has progressed through a series of generalized carnivores; with each step forward, the basic feeding mechanism has improved, and the potential for adaptive radiation has increased (Schaeffer and Rosen, 1961). Although this progression has been marked by periodic bursts of specialized offshoots, the primary stem, the generalized carnivore, has remained relatively conservative (Gosline, 1959).

The generalized predator, in simplified form, has a large mouth and is adapted to directly approach, and seize, prey that are fully exposed to the attack. Its prey are small enough to be manipulated, yet large enough to be grasped; moreover, the prey are not sealed in heavy armour, nor do they carry strong spines, spicules, or other noxious components for which the unspecialized digestive tract of the generalized predator is maladapted. Although even the most primitive of today's predators have acquired at least some feeding specializations, the closer one approximates this simplified form, the closer its feeding habits fit this description.

With the generalized predaceous feeding mechanism being a relatively conservative morphological link between periods of adaptive radiation in actinopterygian fishes, one would expect

conservative predatory behaviors to be associated with this morphology, and just such behaviors are centered around nocturnal and crepuscular feeding habits. The nocturnal habit involves mostly predation on small, motile crustaceans, the crepuscular habit mostly predation on smaller fishes. Together, crustaceans and fishes are the two major types of prey taken by the generalized predator.

Nocturnal and crepuscular habits among generalized carnivores are discussed separately in the following sections. The separation is artificial, as is the delimitation of a third category, that dealing with generalized carnivores that feed regularly by day. In fact, as illustrated below, the behavior patterns associated with these three types of activity are closely interrelated.

Generalized Carnivores as Nocturnal Predators

Early in the evolving relation between fishes and their prey, the evolutionary lines of many small, vulnerable organisms probably increasingly shifted activity to periods of darkness. There scarcely could be a more elementary solution for animals threatened by active, visually orienting predators. And because effective defense adjustments in prey pressure predators to modify their offense, it seems certain that various predators early aquired means to follow their prey into the night. Thus, in predatory fishes the nocturnal habit itself would be a specialization, but a specialization probably adopted in early preteleostean times that has permitted much of the continued widespread success of the generalized predaceous feeding mechanism.

The smaller generalized carnivores on reefs today find their major prey among the abundant crustaceans, which, as follows from the above, are mostly nocturnal animals that expose themselves at night (Longley, 1927; and others). Many generalized predators that would feed on these organisms have found nocturnal habits adaptive, because only after dark does their straightforward attack find suitable prey in the required exposed position. In this feeding relation, the relatively small size of the crustaceans undoubtedly has influenced the size of the predatory fishes, most of which are of small to medium size (less than about 300 mm long).

Most nocturnal fishes in Kona prey on benthic crustaceans, especially xanthid crabs; however, a number are adapted to take crustaceans and other forms from the water column. The prey of these fishes are mainly relatively large zooplankters (a broad, perhaps loose concept of the term "zooplankton" is used in this report), like crab megalops, that are most abundant in the water column at night. Adults of most nocturnal planktivorous fishes in Kona do not feed significantly on the many small plankters, like calanoid copepods, that predominate in the water column during both day and night.

The extent to which the more primitive reef fishes feed at night seems not properly appreciated. Nocturnal habits are widespread among basal percoids, whereas diurnal habits tend to be characteristic of certain more specialized offshoots. Even if one considers only families that occur in Kona, all nearshore species of the Kuhliidae, Priacanthidae, and Apogonidae seem to be nocturnal, as are many species among the Serranidae, Carangidae, Lutjanidae, Sparidae, and Mullidae.

Probably the nocturnal habits of these more generalized percoids were inherited from ancestral beryciforms. The Holocentridae are the major representatives of this once diverse order on nearshore reefs today, yet as illustrated by their prominence in Kona, they nonetheless are numerous, widespread, and obviously successful. All of them for which there are data are nocturnal, and there is no reason to believe that this is not a primitive characteristic. The anamalopids, which are the only other beryciforms on nearshore reefs, also are nocturnal (e.g. Harvey, 1922). Presumably these modern beryciforms have competed successfully with nocturnal forms among the more advanced teleosts by having refined certain features that are highly adaptive to feeding in the dark. Thus, although much of their anatomy is essentially that of their ancestors, they have acquired highly specialized features—at least many of them sensory—that have permitted more effective use of this equipment. All other present-day beryciforms live in the twilight zone of middepths or in the deep sea, and their suitability to the diminished light of this habitat suggests that their shallowwater ancestors perhaps were nocturnal (Richard H. Rosenblatt, Scripps Institution of Oceanography, pers. commun.). Perhaps during the Cretaceous certain more specialized beryciforms possessed diurnal habits, much as many specialized perciforms do today. But if so, these

probably did not survive the widespread extinctions that decimated reef communities at the close of the Mesozoic.

If, as suggested, many reef fishes close to the main line of actinopterygian evolution long ago assumed nocturnal habits in answer to the nocturnal habits of their prey, then one is not surprised to find that widespread predator-prey relations are centered around the nocturnal habit and that the participants are mostly among the more generalized members of the reef community. One especially widespread activity pattern is displayed by the many fishes that assemble in schools on or close to nearshore reefs during the day, then disperse at nightfall and feed on small organisms that become exposed after dark. This is the basic activity pattern of many carangids, lutjanids, pomadasyids, and sciaenids—all among the more generalized perciforms (Hobson, 1965, 1968a, 1972, 1973).

In addition to these basal percoids, it is significant that of the relatively few fishes of preacanthopterygian groups associated with modern reefs, many either follow this pattern themselves, or closely relate as predators to other fishes that do (see next section). A diurnally schooling-nocturnally active pattern is especially widespread, if not universal, among the inshore clupeids, order Clupeiformes—as described earlier for *Harengula thrissina*, an exceedingly numerous fish close to shore in the Gulf of California (Hobson, 1965, 1968a). Starck and Davis (1966) found this same pattern in all five clupeids that they studied on reefs in Florida, and I observed it in *Herklotsichthys punctatus* in the Marshall Islands (unpubl. data). Pertinent information on nearshore clupeids is limited because so few investigators have distinguished between diurnal and nocturnal activity; nevertheless, there are at present no data refuting the generalization that these fishes feed at night.

There are fewer of these diurnally schooling, nocturnally active fishes on Kona reefs than on most other tropical reefs, perhaps for reasons discussed earlier (Hobson, 1972). Still, the pattern is well defined there in certain of the mullids, genus *Mulloidichthys*, and in the lutjanid *Lutjanus vaigiensis*, and is especially apparent in the atherinid *Pranesus insularum*, just as in its congener *P. pinguis* of the Marshall Islands (Hobson and Chess, 1973)—both of the preacanthopterygian order Atheriniformes.

Generalized Carnivores as Crepuscular Predators

In the same way that many generalized predators are nocturnal because suitable prey are most available to them after dark, other generalized predators—those that prey mostly on smaller fishes—are primarily crepuscular because that is when these prey become most vulnerable to their mode of attack (Hobson, 1968a). Moreover, just as is true of the nocturnal forms, the crepuscular piscivores, which also are among the more generalized of the reef fishes, experience certain long-established predator-prey relations. Significantly, many of these crepuscular piscivores are members of the same basal percoid families, the Serranidae, Carangidae, and Lutjanidae, that have produced some of the nocturnal predators discussed above. Many of the crepuscular piscivores, however, tend to be larger than the nocturnal species, which might be expected, inasmuch as the nocturnal fishes are among their major prey (Hobson, 1968a). Schools of nocturnal carangids, pomadasyids, mullids and, especially, clupeids, are well-known targets of such piscivores.

During the twilight periods of greatest piscivorous activity (Hobson, 1968a, 1972), these nocturnal fishes are still in their diurnal schools. And although the schools effectively protect them from predators during most of the day (Manteifel and Radakov, 1961; Eibl-Eibesfeldt, 1962; Hobson, 1968a), this protection is reduced during twilight (Hobson, 1968a). At this time of maximum danger from predators, most other smaller reef fishes, both diurnal and nocturnal, are under cover; thus, the schooling fishes, which are still in the water column, become the most numerous prey of proper size exposed to the space-demanding attacks of the generalized piscivores (Hobson, 1968a). After dark, the smaller fishes seem relatively safe from at least most such predators (Hobson, 1973), but during the changeover between day and night, they are vulnerable (Hobson, 1968a; Munz and McFarland, 1973).

The large piscivores are exceptionally abundant in certain parts of the Gulf of California where the diurnally schooling, nocturnally active fishes are numerous (Hobson, 1968a). As suggested earlier (Hobson, 1972), the relatively few such large predators on Hawaiian reefs, compared with most other tropical areas, may relate to the relative dearth in Hawaii of schooling prey.

Thus, a major activity pattern of these large piscivores closely interrelates with a major activity pattern of the smaller nocturnal predators. For this reason, and because so many members of the two groups are closely related taxonomically, it is apparent that the crepuscular pattern probably has had a longevity comparable to that of the nocturnal pattern. A good indication of this long history exists in the Gulf of California, where the day-night activity pattern of the nocturnal clupeid *Harengula thrissina* closely interrelates with the crepuscular activity not only of certain basal percoids, but also of *Elops affinis*, order Elopiformes, a member of the most primitive of all extant teleostean genera (Hobson, 1968a).

Generalized Carnivores as Diurnal Predators

Thus, nocturnal or crepuscular habits are adaptive for many generalized carnivores. Others with basically the same feeding mechanism, however, have acquired morphological and behavioral characteristics suited to capture small, motile crustaceans and, especially, fishes in daylight. Despite the fact that crustaceans are most exposed to direct attacks at night, and smaller fishes generally are most vulnerable to such attacks during twilight, various predators are equipped to exploit the exceptions to these generalizations.

True, selective pressures applied by generations of visually orienting predators have refined the defense mechanisms that protect so many prey organisms during daylight. But there are occasional lapses in all these defenses when the prey are briefly vulnerable. For example, nocturnal organisms resting under a thin layer of sand occasionally betray their presence by moving. And small fishes that usually are within retreating distance from cover sometimes stray too far into the open; or others, enjoying the security of a school, occasionally drift too far from their fellows. Still others, normally alert to surrounding danger, are momentarily distracted. At such times, these organisms are open to attack. But normally such events fail to occur in the presence of large, free-swimming predators that are actively hunting. Potential prey are sensitive to cues that mark the hunting predator, and take defensive action when a hunter appears—cryptic forms stop moving, others move closer to cover, and schooling forms draw themselves closer together (Hobson, 1965, 1968a). Above all, in this alerted state the prey are less likely to make a defensive mistake. This does happen occasionally, of course, as when large carangids swim slowly among schooling prey for hours during the day without an aggressive move, and then suddenly attack —presumably having sensed a vulnerable target (Hobson, 1968a). Probably this offensive tactic depends on the prey eventually becoming conditioned to the predator's presence, and finally making a mistake. But it seems unlikely that such predators could depend on these relatively infrequent successes. They remain best suited for crepuscular attacks.

The problem of being within striking range when prey are momentarily available during the day because of a defensive lapse is probably best solved by those predators that lie in wait under concealment—the ambushers—or by those that stalk. Both tactics have produced some highly specialized forms that are more appropriately considered in the next section. However, many of those that use concealment to ambush their prey look much like the nocturnal or crepuscular predators discussed above, and so are considered here.

This is especially true among certain basal percoids, like the serranids. For example, many species of *Epinephelus* ambush prey from a concealed position, and much of this activity occurs in daylight (Hiatt and Strasburg, 1960; and others). Most of these predators are cryptically hued for a sedentary existence among rocks or coral—usually they are brown or grey, with the hues often arranged in blotches or spots. Such predators rest unseen until a small organism within striking distance makes a defensive error.

Generalized predators adapted for this tactic are well known to feed regularly during both day and night, as exemplified by certain species of *Epinephelus* (Longley and Hildebrand, 1941; Starck and Davis, 1966; Hobson, 1968a). There is evidence, however, that feeding habits of these predators differ between day and night. In the Gulf of California, *E. labriformis* preys almost entirely on crustaceans at night, but heavily on fishes during the day (Hobson, 1968a). I have already commented on the increased vulnerability of small crustaceans at night; apparently fishes are more vulnerable to the predatory tactics of this fish in daylight. The diurnal piscivorous habit of *Cephalopholis argus* (*Epinephelus argus* of some authors, e.g. Smith, 1971) in Kona is consistent with this probability.

Predators having obvious morphological and behavioral specializations that increase their proficiency as ambushers or as stalkers are considered in the next section.

Specialized Offshoots from the Main Line of Teleostean Evolution

Most fishes inhabiting tropical reefs today, as exemplified by species in Kona, represent specialized offshoots from the main teleostean line.

Predators Specialized to Ambush Prey

As emphasized in the introductory remarks, the categories erected in this discussion overlap. This is especially true of predators that ambush their prey. By using this tactic, predators with the generalized feeding mechanism increase their capacity to capture prey in daylight. But many ambushers, like certain species of *Epinephelus*, are so similar in both morphology and habits to many of the nocturnal and crepuscular forms discussed above that one can only arbitrarily distinguish them as being specialized in this activity. Nevertheless, some forms have retained the generalized feeding mechanism while diverging widely from the primitive form in other respects. And the divergence is based on features that better adapt these fishes for the ambushing tactic.

The synodontids, order Myctophiformes, which are prominent ambushers in Kona, as they are on most other tropical reefs, are products of an evolutionary offshoot that diverged from the main line at a preacanthopterygian level. Thus, the ambushing tactic has had a long history. The scorpaenids, order Scorpaeniformes, and the bothids, order Pleuronectiformes, both of whose Kona representatives include specialized ambushers, belong to groups that diverged from the mainstream near the percoid level (Gosline, 1971; and others). Significantly, the adults of all these forms seem to be primarily piscivorous during the day.

The synodontids, scorpaenids, and bothids that ambush their prey have acquired characteristics that camouflage them as they lie on the sea floor. Clearly, it is important for these predators to go unseen by their victims. In this respect, many of the cirrhitids, order Perciformes, might seem a puzzle. An example from Kona is *Paracirrhites forsteri* (Figure 32), which preys mostly on smaller fishes during the day. Although attacking prey in much the same manner as other ambushers, this colorful fish is clearly visible as it rests in exposed positions on the reef. Selection, in this case, may have in fact favored coloration that attracts attention. Conceivably this could be an effective offensive characteristic, just so long as its use among predators is limited. It is well known that certain small fishes are attracted to conspicuous objects on the sea floor—one needs only to place a small, shiny artifact on the bottom to see this. Perhaps *P. fosteri* actually finds prey among small fishes that approach to investigate its conspicuous features.

Predators Specialized to Stalk Prey

Many predators specialized to stalk prey in the water column belong to groups whose ancestors diverged from the main teleostean line below the percoid level. Characteristically, they have long, attenuated bodies. Among species whose behavior in Kona is described above are the trumpetfish, *Aulostomus chinensis*, and the cornetfish, *Fistularia petimba*—both of the order Gasterosteiformes.

Two other highly specialized stalkers on Kona reefs were not included in the species accounts above because observations on them were infrequent; these are the needlefish, *Strongylura gigantea*, order Atheriniformes, and the barracuda, *Sphyraena barracuda*, order Perciformes. The various species of needlefishes and barracudas are widespread on tropical reefs, and their stalking habits are well documented. Hiatt and Strasburg (1960) reported that *Strongylura gigantea* feeds on small fishes in the Marshall Islands by "drifting up to them and suddenly lashing out with its jaws." On the basis of similar observations in the tropical Atlantic, Randall (1967) reported that needlefishes are almost exclusively piscivorous, and that they "drift slowly into range of one of their prey before making a quick rush." Regarding barracudas, Hiatt and Strasburg (1960) told of *Sphyraena genie* in the Marshall Islands "drifting solitary near the surface stalking its prey" and stated that "it surprises its victim with a sudden lunge." Randall (1967) noted that barracudas in the tropical Atlantic feed primarily on fishes during the day, a statement probably true of at least most stalking predators.

Predators Specialized to Seek Prey in Reef Crevices

Here I am concerned primarily with muraenid eels, order Anguilliformes, and the brotulids, order Gadiformes. Members of both groups, but the eels in particular, have elongated bodies suited to maneuvering through the crevices that honeycomb coral reefs. Their similar morphologies led early Hawaiians to group eels and brotulids together by the generic term *puhi*. There are a number of other secretive forms on Kona reefs—small inconspicuous fishes like the pseudochromid *Pseudogramma polyaccanthus*, which were occasionally visible at night during this study—but because I have little knowledge of their habits they are not considered here.

The muraenid eels are products of an evolution that has diverged widely from the main teleostean line: today they possess many specialized features that equip them for hunting in reef crevices. The primary specializations, for example their exceptionally solid skulls, are adaptive for wedging through small openings, and they can back out of any hole they enter (Gosline, 1959, 1971). Many of the morays, and at least some of the brotulids, for example *Brotula multibarbata* in Kona, are nocturnal; however, other morays are diurnal. Obviously hunting conditions in reef crevices differ between day and night.

Reef crevices are havens for numerous creatures. Many diurnal forms rest there at night, some of them virtually asleep, and many nocturnal forms shelter themselves there in daylight (Hobson, 1968a, 1972). Moreover, most reef animals find refuge in these crevices when they are injured or distressed; obviously, sheltering in reef crevices is adaptive for prey threatened by the many predators on the surface of the reef. But it is equally obvious from their long successful history on tropical reefs that eels have acquired adaptive means to exploit such prey.

Predators with Sensory Specializations That Detect Concealed Prey

In this category I am concerned with the mullids, order Perciformes, which are prominent on Kona reefs. Their distinctive sensory chin barbels permit them to locate prey that go undetected by other fishes. And, like the muraenid eels, above, their numbers include both diurnal and nocturnal forms, as well as species that hunt effectively during both day and night. This fact, and the great diversity in their prey, shows that mullids, with their distinctive modes of feeding, have available to them a broad range of predatory activity denied most other fishes.

Although seeking refuge under rocks, algae, or sand is adaptive for many small animals approached by a predator, this tactic probably plays to the advantage of some mullids. For example, the diurnal *Parupeneus chryserydros* preys mostly on small diurnal fishes that typically take cover when threatened. This mullid may use its exceptionally long barbels not only to locate such animals, but also to drive them into the open.

Many small organisms that seek cover when threatened rest in the same refuges when they are inactive, and at such times may be prey for other mullids, notably *P. bifasciatus*. This species seems to feed with equal effectiveness day and night, although its food habits differ between these two periods. In this respect, a comparison with the serranid *Epinephelus labriformis* in the Gulf of California is insightful. As noted above, *E. labriformis* also feeds regularly day and night, taking mostly crustaceans after dark and small fishes in daylight; thus, its food habits agree with the generalization that crustaceans are most vulnerable at night, and fishes most vulnerable in daylight. *Parupeneus bifasciatus* seems to be a successful exception to this generalization, because it takes fishes more often at night than during the day and crustaceans more during the day than at night. Apparently, *P. bifasciatus* is specialized to capture prey that rest under cover, safe from predators with generalized feeding equipment.

Thus, at least some mullids find prey among animals that have sheltered themselves in the reef, just as do some of the muraenid eels, so that, like the eels, they have gained advantage from what generally are successful defensive behaviors in their prey. But whereas the eels probe deep into reef interstices, the mullids confine their activity to the superficial covering on the reef.

Predators Specialized to Take Prey Among the Plankton During the Day

There are clear distinctions between diurnal and nocturnal planktivorous fishes on coral reefs, with the diurnal species inactive at night and the nocturnal species inactive during the day (Hobson, 1965, 1968a, 1972; Starck and Davis, 1966). Emery (1968) showed that the composition of

plankton over reefs in Florida also differs between day and night, a fact undoubtedly related to the diurnal-nocturnal dichotomy among the planktivorous fishes. As described above, planktivorous fishes that feed in the water column at night, for example *Myripristis* and *Apogon,* have the generalized carnivore's large mouth and prey largely on the relatively large plankters, like crab megalops, that are mostly in the water column above the reef after dark.

Although a large array of plankters inhabit the water column during the day, generally they seem too small for adults of the large-mouthed nocturnal planktivores. Significantly, diurnal planktivores all have a small mouth, and their major prey, calanoid copepods, are generally smaller than the prey of their nocturnal counterparts. Moreover, diurnal planktivores among adult reef fishes generally are among the more advanced teleosts, having attained, or passed, the percoid level of development. There are no basal percoids among the prominent diurnal planktivores in Kona, but in the tropical Atlantic certain serranids, lutjanids, and pomadasyids specialized in this habit are numerous (Starck and Davis, 1966; Randall, 1967). Most diurnal planktivores on coral reefs, however, are among the higher Perciformes. These include the pomacentrids, which probably include a higher proportion of planktivorous species than any other major family of coral-reef fishes. The balistids, order Tetraodontiformes, are among the most advanced teleosts and include several specialized diurnal planktivores: species of *Melichthys* and *Xanthichthys ringens* are prominent on coral reefs over much of the tropical world.

Many unrelated species that forage on zooplankton in the water column during the day display convergent morphologies. Features characteristic of these fishes were identified by Davis and Birdsong (1973), who did not distinguish between diurnal and nocturnal forms, however. Drawing examples from the tropical Atlantic Ocean, they illustrated certain unrelated planktivorous fishes, for example *Paranthias furcifer* (a serranid) and *Chromis cyanea* (a pomacentrid), that, on casual inspection, look more like one another than they do members of their own families that feed on the benthos. The similarity among these unrelated forms is based mainly on their common increased tendency toward a fusiform body, a deeply incised (forked or lunate) caudal fin, and a small, upturned mouth that gives their heads a characteristic appearance. Presumably diurnal planktivores that tend toward a more fusiform body and deeply incised caudal fin—both well-known characteristics of rapid-swimming oceanic fishes—can swim faster than relatives in which these tendencies are less developed. Considering the many active predators at large during the day, increased speed clearly is adaptive for small reef fishes that swim at that time in open water, high above the sheltering reef. The advantage of the upturned mouth may be indirect: Rosenblatt (1967) acknowledged Walter A. Starck II for pointing out that this mouth construction gives the fish a shortened snout, which permits close-range binocular vision—an obvious advantage in capturing tiny organisms in the water column. A number of diurnal planktivorous fishes in Kona possess one or more of these characteristics, as described and illustrated above (e.g. Figures 38 and 40).

Significantly, none of the nocturnal planktivores in Kona tend toward having either a more fusiform body, or a more deeply incised caudal fin. In fact, planktivorous squirrelfishes of the genus *Myripristis* are actually deeper bodied than their bottom-feeding relatives of the genus *Holocentrus,* and the caudal fins of most are less deeply incised (compare, for example, Figures 11a and 14). If, as suggested above, these features gain selective advantage in the planktivores by providing added speed to elude predators in open water, then their absence among forms that rise into the water column after dark is consistent with the contention (above, and Hobson, 1973) that small free-swimming fishes face a much diminished threat from predators at night. Many of the nocturnal species, including species of *Myripristis,* have the sharply upturned mouth; but it is a large structure, as noted above, suited to taking the larger zooplankters that appear in the water column after dark.

Not all of the diurnal planktivores in Kona tend toward fusiform bodies, deeply incised caudal fins, or sharply upturned mouths. None of these features occur in the planktivorous chaetodontids, for example *Hemitaurichthys zoster* (Figure 28a), which nevertheless are well suited to feed on copepods, and other tiny zooplankters in the water column by day. Obviously many conflicting pressures have differentially affected the morphologies of the various fishes that forage on tiny organisms in the mid-waters.

Predators Specialized to Prey on Benthic Invertebrates During the Day

A wide variety of fishes prey on benthic invertebrates during the day. They include most of the labrids, chaetodontids, balistids, canthigasterids, monacanthids, ostraciontids, and tetraodontids, as well as many of the pomacentrids, blenniids, and others—all of them higher perciforms or tetraodontiforms. Their prey are among the more prominent invertebrates on the reef, including such sessile forms as sponges, coelenterates, and tunicates; and also various slow moving animals like echinoids and gastropods. Typically, these prey are fortified with toxic or noxious components, like spines, spicules, nematocysts, or tough, fibrous components; or they are encased in heavy armour. Because of these defensive features, fishes that prey on such forms must have specialized feeding structures or techniques—the unspecialized feeding apparatus of generalized predators is maladapted for this task. Also unavailable to generalized predators are the many very small organisms whose capture requires delicate manipulations or movements for which large-mouthed fishes are unsuited. Moreover, many of these prey are diurnally cryptic or secretive, thus requiring still additional specializations to capture them in daylight.

Thus, fishes that successfully feed on most benthic reef invertebrates during the day are advanced species whose evolution has been mostly one of perfecting means to feed in daylight on prey that are beyond the capacity of fishes with generalized feeding equipment. Certain mullids, discussed above, are adapted to feed on many of these prey, but mullids use nonvisual means, whereas fishes considered here are primarily visual feeders.

These are fishes that have passed the percoid level of development. The evolution of the percoid morphology, especially with its highly adaptive feeding mechanism, gave fishes added potential to adjust to a wide variety of feeding situations. But although percoids appeared first during the Cretaceous (Patterson, 1964), not until modern reef communities appeared during the Eocene (Newell, 1971) does it appear they began to fully realize this potential.

Bakus (1964, 1966, 1969) concluded that the secretive habits and defensive structures of many benthic invertebrates on coral reefs today, including sponges, didemnid tunicates, and others, are the result of predation pressures from fishes. Whether or not this is so, certainly the array of specialized feeding habits and structures that characterize diurnal bottom-feeding fishes on coral reefs are mostly adaptations which cope with specific defensive characteristics of their prey. Because predation pressures lead to defensive adjustments in prey, and these in turn stimulate further offensive modifications in predators, it is not surprising that the diverse array of defenses in benthic invertebrates today is matched in the fishes that feed on them by an equally diverse array of solutions. These solutions to invertebrate defenses are manifest in the extremely varied feeding structures and behaviors that occur among diurnal fishes. Most diurnal fishes specialized for diets of benthic invertebrates have relatively small mouths, but beyond this their feeding morphologies have diverged widely.

Sessile invertebrates seem to be significant prey only during the day, perhaps because an animal must move to be sensed by most predaceous fishes at night (Hobson, 1968a). Thus, the few highly specialized fishes that feed on sponges are strictly diurnal. In Kona, the chaetodontid *Holacanthus arcuatus* feeds on some of the larger sponges that encrust in exposed locations on rocks, whereas the zanclid *Zanclus canescens* uses its elongated snout to feed on some of the smaller sponges that are attached within crevices or depressions on the reef. Randall and Hartman (1968), in studying sponge-feeding chaetodontids and monacanthids in the West Indies, noted that sponges cannot be digested by most fishes, and concluded that these organisms have become available as food for only a few highly specialized teleosts in geologically recent times.

Some diurnal predators, for example *Forcipiger flavissimus*, *Chaetodon auriga*, and *C. fremblii*, among chaetodontids in Kona, habitually tear off pieces of larger sessile invertebrates, including polychaetes, tunicates, and alcyonarians. The analogy drawn above between the snout and jaws of *F. flavissimus* and a pair of needle-nosed pliers underscores the suitability of this fish's feeding morphology for its feeding habit.

One of the most obvious potential foods for carnivorous bottom-feeding fishes on coral reefs would seem to be the corals themselves. Nevertheless only some of the most advanced teleosts exploit this resource. In Kona, coral eaters include certain chaetodontids, pomacentrids, and blenniids (all higher Perciformes) and certain

monacanthids and tetraodontids (all Tetraodontiformes). In pointing out that coelenterates are not food for fishes in most marine communities, Hiatt and Strasburg (1960) cited various specialized features of fishes that prey on corals in the Marshall Islands: for chaetodontids and monacanthids that snip off individual polyps, they listed the produced snouts, small terminal mouths, and fine protruding incisiform teeth; for tetraodontids and balistids that bite off larger pieces of coral, they noted very heavy, strong dentition. All fishes that feed on coral, including those that feed heavily on coral mucus, seem to be diurnal. Obviously a predator that bites off large chunks of coral, or which scrapes away mucus, would find diurnal habits adaptive—its food is equally accessible day or night, and its own activity would benefit from daylight. On the other hand, the polyps of some coral species are most expanded at night, suggesting that perhaps predators that would snip them off might find them most accessible after dark; however, the precise manipulations involved in this activity probably require the light of day, because without exception all such predators are diurnal.

Daylight and precise manipulations also seem required of predators that pluck tiny cryptic organisms, notably amphipods, from amid benthic cover. An example from Kona is the labrid *Anampses cuvier*, whose prey are amphipods and other organisms too small for large-mouthed generalized predators of comparable size. Taking such prey requires a specialized tactic and feeding mechanism. Characteristically such predators hover within a few centimeters of the substratum, inspecting the surface. When they spot prey —perhaps through movement or an unusual contour—they take it in a characteristic plucking manner.

Probably this way of plucking tiny prey from a substratum preadapted precursors of those fishes that are specialized as cleaners. Most cleaner fishes, which include certain labrids, pomacentrids, and chaetodontids, pluck various materials, mostly ectoparasitic crustaceans, from the bodies of other fishes. Possessing both the necessary techniques and morphology, certain fishes in this category were prepared to adopt the cleaning habit when their concept of a suitable feeding substratum broadened to include the bodies of other fishes (Hobson, 1971). A few species, like *Labroides phthirophagus* in Kona, are specialized as cleaners, having refined both their feeding morphologies and techniques to more efficiently practice this habit. All known cleaner fishes are diurnal.

Most of the invertebrate prey of diurnal fishes are insignificant as prey of nocturnal fishes. However, the specializations that permit certain diurnal fishes to seek out secretive prey in daylight make available to them at that time some of the forms—motile crustaceans in particular—that are important prey of various generalized predators after dark. For some fishes, the adaptations that permit them to take crustaceans and other forms from under reef cover in daylight are morphological. Thus, the chaetodontid *Forcipiger longirostris* and the labrid *Gomphosus varius* both have elongated snouts with which they reach deep into reef crevices for crustaceans. In other fishes the adaptations that make secretive prey available are more strictly behavioral. Thus, the labrid *Thalassoma duperrey* follows close to the feeding jaws of large herbivores and other fishes that disturb the substratum, and snaps up tiny crustaceans driven from cover. This behavior is widespread, occurring in other wrasses in Kona and also in the Gulf of California (Hobson, 1968a). Some species lower on the evolutionary scale seem to have similar behavior: as suggested above, the carangid *Caranx melampygus* may enjoy this advantage by following the mullid *Parupeneus chryseydros*, as may the aulostomid *Aulostomus chinensis* by accompanying grazing schools of acanthurids—in these two situations, however, the prey seem to be mostly small fishes.

Some diurnal predators excavate buried prey, as when the labrid *Coris gaimard* overturns small stones with its snout and feeds on animals thus exposed. And in the eastern Pacific the balistid *Sufflamen verres* uncovers prey buried in the sand by exposing them with a jet of water from its mouth, or by rapidly undulating dorsal and anal fins while lying on its side, thereby generating currents that sweep the sand away (Hobson, 1965, 1968a). Similarly, the ostraciontid *Lactophrys triqueter* in the tropical Atlantic by jetting water from its mouth uncovers prey buried in the sand (Longley, 1927).

Related Problems of Species Recognition.—The enormous potential for varied feeding adaptations in these advanced teleostean groups has led to the occurrence on most coral reefs of large numbers of closely related species that seem to have diverged from one another chiefly on the basis of differing food habits. For example, 14 species of the genus

Chaetodon occur together on Kona reefs—all very similar in general body form, but with distinctive differences in diet and related morphology. Obviously, such situations can exist only if, in addition to having acquired adaptations suited to specialized diets, closely related forms have also acquired effective barriers to interbreeding. Central to this is the ability of each individual to recognize others of its own kind, which probably relates to the circumstance that most species in this category have highly visible species-specific color patterns.

It is logical that diurnal fishes would employ visual cues to identify one another. But the distinctive nocturnal colorations of many chaetodontids suggest that members of some species need to recognize each other after dark as well. Nocturnal colorations that occur among chaetodontids in Kona tend to accentuate a contrast, thus making them more visible at lower light levels (e.g. Figures 28a and b; 29a and b). Although the nocturnal colorations of some fishes, such as those that become mottled, make them more difficult to see in the dark (Schroeder, 1964), certain chaetodontids in Kona seem to be effecting a nocturnal display. This phenomenon appears most pronounced among fishes in the present category, but others show it as well; for example, in Kona certain of the nocturnal squirrelfishes, *Holocentrus* (Holocentridae: Beryciformes) display characteristic white bars or spots at night that are more visible under reduced light than their daytime colorations would be (e.g. Figure 12a and b). Probably one can generalize only to the extent that distinctive day/night colorations in coral reef fishes reflect distinctive day/night situations.

Fishes Specialized to Feed on Vegetation

Vegetation, which carpets much of the rocky sea floor inshore, would seem ready food for fishes. Yet relatively few species utilize this resource, even though, as in Kona, they often predominate on tropical reefs. The herbivorous habit is an advanced trait among marine fishes, a fact recognized by Hiatt and Strasburg (1960).

In general, herbivorous fishes on coral reefs share many characteristics with the diurnal predators that are specialized to prey on benthic invertebrates, discussed in the previous section. Like the fishes grouped together in that category, at least most coral reef herbivores are active by day and relatively inactive at night; furthermore, they too tend to be colorful animals that have small mouths which are part of highly evolved feeding systems. In fact, several families of fishes span both categories; for example, the Chaetodontidae, Pomacentridae, Blenniidae, Balistidae, Monacanthidae, and others include gradations of species from some that are strictly carnivorous, to others that feed on both plants and animals, to still others that are strictly herbivorous. Within these groups, which have favored plasticity in feeding habits and structures, it seems that characteristics adaptive to plucking benthic invertebrates from the sea floor have been modified in some species for grazing on plants.

Nocturnal Activity Among Advanced Teleosts

Not all the more advanced fishes are diurnal. The chaetodontid *Chaetodon lunula* seems to be nocturnal in Kona, and at least some of its congeners—notably *C. quadrimaculatus* and *C. auriga*—may feed to some extent after dark. But these are exceptional cases in an overwhelmingly diurnal group. As suggested above, nocturnal activity in these instances may relate to competition among the exceptionally large number of *Chaetodon* species that cooccur on Kona reefs.

Nocturnal habits cannot be regarded as exceptional where they occur among the diodontids, however, because night feeding seems to be the rule in this family. And these members of the order Tetraodontiformes are among the most highly evolved of all reef fishes. The prey of *Diodon hystrix* and *D. holocanthus* in Kona —large echinoids, gastropods, and pagurid crabs—are more exposed at night than during the day. And because they are relatively large and move at least intermittently after dark, one can predict they would be suitable quarry for nocturnal predators having means to crush heavy armour. These are large prey, so a predator must carry its crushing mechanism in its mouth, rather than in its throat—as do many of the labrids and other predators that feed on smaller mollusks and echinoids during the day. The highly evolved diodontids accomplish this job with their powerful crushing jaws, but the problem has also been solved at a more primitive level by certain basal percoids. In Kona, the nocturnal sparid *Monotaxis grandoculis*, with its molariform dentition, has feeding habits similar to those of the diodontids, but with less emphasis on heavily armoured forms. Clearly, the diodontids, with more powerful jaws and heavier dentition, are better adapted

than the sparids for this particular task. Of even more primitive stock than the sparid, the muraenid eel *Echidna zebra* has crushing dentition, but its prey seem to be primarily large crabs that it takes regularly from reef crevices in daylight. There is no evidence that it can crush the heavy gastropods so prominent in the diets of the more advanced sparids and diodontids.

CONCLUSIONS

1. The feeding relationships of fishes on coral reefs in Kona, Hawaii, follow essentially the same pattern as do feeding relationships of fishes on coral reefs elsewhere.

2. Nocturnal habits have had a long history in teleostean fishes, and are widespread among the more generalized forms, including many of the clupeids, holocentrids, serranids, kuhliids, priacanthids, apogonids, lutjanids, and others. These large-mouthed predators find night feeding adaptive because that is when their prey—mostly small, motile crustaceans—are in exposed locations and thus vulnerable to their straightforward attack.

3. Piscivorous predators that have a generalized feeding mechanism, and which attack with a straightforward charge, for example certain large carangids, are mostly crepuscular.

4. Certain piscivorous predators that have a generalized feeding mechanism feed effectively during the day, as well as during twilight, by ambushing or stalking their prey. The ambushers, which include certain synodontids, serranids, scorpaenids, and bothids, typically have cryptic morphology, coloration, and behavior. The stalkers, which include the aulostomids, fistulariids, belonids, and sphyraenids, typically have long, attenuated bodies.

5. In acquiring features adaptive for hunting in reef crevices, muraenid eels have become highly successful, capitalizing on the otherwise effective shelter-seeking habits of small reef animals. Although many small reef animals become more vulnerable to eels when they shelter in reef crevices, they find these refuges adaptive when resting, injured, or distressed, because they are relatively safe here from the even greater threat from predators that exists on the surface of the reef.

6. The mullids use their distinctive sensory barbels to locate prey that are sheltered under the superficial covering of the reef and adjacent sand. Some mullids are best adapted to capture such prey at night, others to capture such prey in daylight, and some feed effectively during both day and night. At least some use their barbels not only to detect prey, but also to drive them into the open.

7. Most fishes on Kona reefs, like fishes on coral reefs elsewhere, are among the more recently evolved teleosts, having reached, or passed, the percoid level of structural development.

8. The adaptability of the perciform feeding apparatus has given rise to a wide variety of forms that have diverged from one another primarily on the basis of differing food habits. Much of this diversity has resulted from adaptations that cope with specific defensive characteristics of the organisms on which these fishes feed.

9. Just as nocturnal and crepuscular habits predominate among the more generalized coral-reef fishes, diurnal habits predominate among the more advanced, specialized forms, including most of the higher Perciformes, and Tetraodontiformes. Some of the most advanced of all, however, including the diodontids, are nocturnal.

10. Some higher teleosts, including certain chaetodontids, labrids, and balistids, have specializations that permit them to capture, during daylight, nocturnal forms hidden under cover. Such prey include forms like motile crustaceans that expose themselves at night, and at that time become the major prey of generalized nocturnal fishes.

11. Some advanced teleosts, including certain chaetodontids, labrids, and pomacentrids, are specialized to pluck tiny prey, such as amphipods, from among vegetation and other benthic cover. These prey are too small, and too cryptic, to be taken after dark or by predators with a large mouth. This plucking habit preadapted certain species for cleaning ectoparasites and other material from the bodies of other fishes.

12. Fishes that prey mostly on sessile invertebrates, like sponges and coelenterates, are highly evolved diurnal species, including certain chaetodontids, pomacentrids, balistids, and monacanthids. These predators have specialized feeding structures and techniques that handle various noxious or toxic defensive features in their prey, including spines, spicules, nematocysts, tough fibrous tissues, and heavy armour. And they take these sessile animals in daylight because only moving prey are effectively sensed by visually feeding predators after dark.

13. Characteristics developed in feeding on sessile benthic invertebrates have been modified in some fishes for grazing on benthic vegetation. Thus, many families, for example the Chaetodontidae, Pomacentridae, Balistidae, and Monacanthidae, include some strictly carnivorous forms that prey on benthic invertebrates, other forms that feed on both benthic invertebrates and vegetation, and still others, strictly herbivorous, that only graze on benthic vegetation.

14. On coral reefs there is no sharp distinction between fishes that feed on sessile invertebrates and those that graze on benthic vegetation: species in both categories tend to be colorful diurnal fishes with a small mouth that is part of a highly evolved digestive apparatus.

15. The plasticity in feeding habits and structures characteristic of higher teleosts that feed on benthic organisms has led to the multiplicity of closely related, and morphologically similar species that live together on coral reefs. This situation could not have evolved without effective barriers to interbreeding, which in turn requires that individuals recognize others of their own kind from among many very similar forms. This requirement has been met by having developed highly visible, species-specific color patterns. The distinctive nocturnal color patterns of some forms, for example *Zanclus* and certain chaetodontids, indicate that, although they are diurnal, certain of them need identifying features at night, as well as during the day.

16. The small mouth of higher teleosts is adaptive for feeding on the smaller plankters, like calanoid copepods, that compose the vast majority of organisms in the water column. This characteristic distinguishes diurnal planktivores, including certain pomacentrids, chaetodontids, and balistids, from the nocturnal planktivores, which include certain holocentrids and apogonids. Most nocturnal planktivores have the larger mouth of the generalized predators, and most of them feed primarily on the larger plankters, like crab megalops and mysids, that are most numerous in the water column over the reef at night.

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THE EFFECTS OF DIETARY α-TOCOPHEROL AND TUNA, SAFFLOWER, AND LINSEED OILS ON THE FLAVOR OF TURKEY

L. CRAWFORD,[1] D. W. PETERSON,[2] M. J. KRETSCH,[1] A. L. LILYBLADE,[2] AND H. S. OLCOTT[3]

ABSTRACT

Turkeys were fed varying levels of α-tocopherol acetate and oils containing linolenates (linseed and tuna oils). As expected, these oils caused a fishy flavor to develop in the turkey carcass, and α-tocopherol fed concomitantly, greatly retarded development of this fishy flavor, but did not affect the uptake of linolenates by the turkey carcass. These and other observations pointed to the conclusion that linolenates do not by their simple presence in turkey carcass cause fishy flavor, but that perhaps their in vivo and/or postmortem oxidation are responsible for the development of this flavor.

Several investigators have reported that fishy flavors develop in poultry carcass when diets are supplemented with oils, such as linseed oil (Klose et al., 1951) and fish oil (Neudoerffer and Lea, 1966, 1967, 1968; Miller et al., 1967a, 1967b; Miller and Robisch, 1969; Dreosti, 1970; Opstvedt, Olsen, and Urdahl, 1970; Opstvedt, Nygard, and Olsen, 1970, 1971). The latter investigators showed that this off flavor is related to the linolenate content of the oil, especially the long chain homologues. Miller and Robish (1969) showed that fishy flavors were eliminated with the withdrawal of fish oils and substitution of a more saturated fat (like tallow) in the diet. Lineweaver (1970) reported that practical experience has shown that the amount of fish oil in the diet of poultry should not exceed 0.3% if fishy flavors are to be avoided. However, it was not clear whether the specific character of the oil (ω3 fatty acid content) was a factor to be considered.

Lea et al. (1966), Dreosti (1970), and Opstvedt et al. (1971) reported that antioxidant-treated fish meal is more likely to cause fishiness than untreated meal. They reasoned that the unsaturated fatty acids of the untreated meal become oxidized and, perhaps, polymerized, thereby becoming unavailable for uptake in the tissue.

The research of Mecchi, Pool, Beham, Hamachi, and Klose (1956) showed that the stability of turkey fat closely paralleled the tocopherol content of the fat. Other work by Mecchi, Pool, Nonaka, Klose, Marsden, and Lillie (1956) whereby chickens and turkeys were fed varying levels of dietary tocopherol, further substantiated that in fact tocopherol uptake was possibly singularly important to the stability of carcass fat. These findings are corroborated in more detailed studies by Webb, Marion, and Hayse (1972) and Webb, Brunson, and Yates (1972).

Dreosti (1970) and Opstvedt et al. (1971) reported that dietary α-tocopherol acetate supplementation (above levels required to prevent nutritional disease) significantly reduced fishy flavors in poultry fed fish oils.

It is clear that dietary oils containing ω3 fatty acids do in some way contribute to fishy flavors in poultry and that α-tocopherol acetate supplementation reduces the development of this flavor. It is not clear how ω3 fatty acids, when ingested by poultry, result in fishy flavored carcasses or how α-tocopherol reduces the development of this flavor. This paper reports on the fatty acid composition of extracted lipids and on the flavor of the meat from turkeys fed fish oil and linseed oil to 6 wk and to 8 wk of age using safflower oil or beef fat to bring diets into lipid isocaloric balance. Supplemental tocopherol acetate was added to some of the diets. The flavor of adult turkeys fed tuna oil for 2 wk was also observed.

While it is not a practice to raise turkeys to only 6 and 8 wk of age or to feed fish oil midstream for only 2 wk, it was convenient and expedient for the present study. Additionally, observations can be made on the relative uptake of dietary fats and the influence of metabolic rate.

EXPERIMENTS

Oils

Linseed oil, refined safflower oil, freshly rendered beef fat, and fresh polished tuna oil (albacore) were obtained unstabilized. The oils were

[1]Western Regional Research Laboratory, Agricultural Research Service, U.S. Department of Agriculture, Berkeley, CA 94710.
[2]Department of Avian Science, University of California Agricultural Experiment Station, Davis, CA 95616.
[3]Institute of Marine Resources, University of California, Davis, CA 95616.

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deaerated under vacuum and twice flushed with nitrogen. To part of each oil was added 0.3125% ethoxyquin (this will give 125 ppm when added to diet). The stabilized oils were again evacuated, flushed under nitrogen, and stored at −26°C until use. The rendered beef fat was stored at −26°C until used.

Feed

The following basal diet was used in the feeding of turkeys:

Ingredients	*% of diet*
Soybean oil meal (50%)	50.00
Mineral mix	2.58
Vitamin mix (in corn starch)	1.00
$CaHPO_4 \cdot 2H_20$	1.70
$CaCO_3$	1.90
Choline Cl (50%)	0.40
DL-Methionine	0.20
Ground corn	38.42

Diets contained 10 mg vitamin E (*dl*-α-tocopherol acetate) per kilogram and 0.66 ppm sodium selenite. Oils were preweighed and stored at −26°C under nitrogen before incorporation into diets. Diets were mixed with the oils every 1 or 2 wk and stored in a refrigerator and fed fresh daily.

Diets and Feeding

Experiment I

Eighty White Broad Breasted poults (unsexed) were fed chick starter (about 7% fish meal) on day 1. On days 2 and 3, they were fed one-half starter and one-half basal diet. On day 4, they were divided into eight groups of 10 turkeys each, equally distributed by weight, and fed to 6 wk of age on the following experimental diets:

Group	*Oil supplement to basal diet*[1]
1	4% SO
2	4% SO + 125 ppm EMQ
3	1% SO + 3% LO
4	1% SO + 3% LO + 125 ppm EMQ
5	3.5% SO + 0.5% TO
6	3.5% SO + 0.5% TO + 125 ppm EMQ
7	3% SO + 1% TO
8	3% SO + 1% TO + 125 ppm EMQ

[1]SO = safflower oil; EMQ = ethoxyquin, an antioxidant; LO = linseed oil; TO = tuna oil.

Experiments II and III

Eighty-one White Broad Breasted poults were obtained sexed (male only) for Experiments II and III. Starter diet containing 7% fish meal was fed day 1, and one-half starter and one-half basal diet were fed on days 2 and 3. On day 4, the poults were divided into nine groups of nine turkeys each, equally distributed by weight. Groups 1 through 8 were fed the experimental diets described below for 8 wk. These turkeys constituted Experiment II. Group 9 was fed the basal diet without oil supplementation to 14 wk of age and was then divided into three groups of three turkeys each which were designated as Groups A, B, and C. For 2 wk (until 16 wk of age), Group A was fed Diet 1 (control 4% beef fat) and Groups B and C were fed Diets 3 and 5 (3% beef fat + 1% tuna oil and 2% beef fat + 2% tuna oil), respectively. These turkeys constituted Experiment III.

Group	*Oil supplement to basal diet*[1]
1	4% BF
2	3.5% BF + 0.5% TO
3	3% BF + 1% TO
4	3% BF + 1% TO + 200 mg vitamin E/kilogram
5	2% BF + 2% TO
6	2% BF + 2% TO + 200 mg vitamin E/kilogram
7	3% SO + 1% TO
8	2% SO + 2% TO
9	No oil supplement until 14 wk of age

[1]BF = beef fat; TO = tuna oil; vitamin E = *dl*-α-tocopherol acetate; SO = safflower oil.

Sampling and Analysis

All turkeys were sacrificed at the appropriate time by cutting the jugular vein with an electrified knife and bleeding for 2 min. The turkeys were then scalded at 60°C, defeathered, eviscerated, dressed, packed in ice overnight, vacuum sealed, blast frozen, and stored at −30°C for about 4-6 wk. All birds were halved in the frozen state, with half being reserved for chemical analyses and half for baking and subsequent organoleptic analyses.

The halves for chemical analyses were thawed overnight in a 2°C cold room. Thighs and breasts were removed and minced individually after removal of skin and subcutaneous fat. Minced thighs and breasts from individual birds were

wrapped in Saran[4] film and aluminum foil, identified, and stored at −30°C until analyzed.

Oil content was determined on composites of 18-g samples of the individual thighs and breasts from each bird by the modified method of Smith, Ambrose, and Knobl (1964). Methyl esters for gas-liquid chromatography (GLC) analyses were prepared from the same oil extract by the method of Metcalfe, Schmitz, and Pelka (1966). The GLC column was 10% diethylene glycol adipate on Gas Chrom Q. GLC conditions were as follows: column, 196°C; injector, 250°C; flame ionization detector, 300°C; carrier gas flow, 24.6 cm^3/min.

Organoleptic analyses for the turkeys in Experiment I were performed by ranking. The panelists ranked four samples per session (of which one sample was a control). Comments about off flavors, if present, were solicited (e.g., fishy, oxidized, rancid, etc.). In Experiments II and III, organoleptic analyses were performed by scoring, using a balanced incomplete block technique. Analyses of variance and a Duncan multiple range test were calculated for Experiment II. Regression equations were calculated for breast and thigh meat and skin for Experiment III.

RESULTS AND DISCUSSION

Experiment I

All turkeys in Experiment I seemed to have grown normally and to have been in good nutritional health. The mean dressed weight was 991 g, with no significant weight differences between groups.

Table 1 gives the results of GLC analyses and lipid content (grams/100 g) of breast and thigh meat from the turkeys fed linseed and tuna oils to 6 wk of age. As expected, the thigh contained nearly twice the amount of lipid as the breast, (about 2% and 1% extracted lipid, respectively). The distribution of the methyl esters of fatty acids showed consistently higher percentages of C16:0, C18:0, C20:4, C22:5, and C22:6 in the breast, but higher C18:3 (when present in the diet), C18:2 and C18:1 in the thigh for all treatments. The lipid composition of the leg and breast reflect generally that of the dietary oils.

Results of organoleptic evaluation of the turkeys are reported in Table 2. The scoring (by rank) shows that 1% tuna oil imparts off flavor (slight) in breast and thigh meat and somewhat the same trend is indicated for odor evaluation, especially in the breast meat. But no clear trend is indicated for the skin. In general, flavor was judged as excellent. Ofttimes, there were no clear differences in a given set of comparisons. There were only a few scattered comments that described the flavor as fishy. No consistent differences were found between samples with and without ethoxyquin.

The lack of the development of positive fishy flavor in this experiment was unexpected since the oils fed to the turkeys contained high levels of linolenic acid (linseed oil, ca. 57% C18:3 ω3) or one of its longer-chained homologues (tuna oil, ca. 32% C22:6ω3). Fishy flavors have been induced in poultry by other investigators using oils that contained far less linolenates than used in this exper-

[4]Reference to a company or product name does not imply approval or recommendation of the product by the U.S. Department of Agriculture or the National Marine Fisheries Service, NOAA, to the exclusion of others that may be suitable.

TABLE 1.—Methyl ester fatty acid composition[1] of linseed oil and tuna oil and lipids extracted from turkeys[2] fed to 6 wk of age diets containing varying levels of safflower, linseed, and tuna oils with and without ethoxyquin.

Fatty acid	Linseed oil	Tuna oil	1B	1T	2B	2T	3B	3T	4B	4T	5B	5T	6B	6T	7B	7T	8B	8T
C16:0 + Iso C16:0	5.3	14.2	18.4	12.1	18.2	13.6	19.0	11.5	15.7	11.1	17.5	12.5	19.0	14.0	18.5	13.0	17.5	13.1
C18:0	3.8	5.5	12.3	8.4	13.0	9.0	14.9	10.1	11.9	6.7	12.8	8.5	12.6	7.5	10.3	8.9	9.5	5.7
C18:1	18.1	15.8	10.2	13.9	9.1	16.6	11.4	15.7	14.6	18.8	10.3	14.2	9.5	14.8	9.3	13.7	11.7	17.3
C18:2	15.0	4.8	37.8	52.0	40.3	47.1	28.6	35.3	33.5	36.9	33.7	49.2	34.2	48.5	32.5	46.0	38.8	48.0
C18:3ω3	57.8	—	—	—	—	—	4.1	14.6	10.5	19.6	—	—	—	—	—	—	—	—
C20:4ω6	—	3.0	12.0	6.3	10.1	5.6	7.1	4.0	4.3	1.9	8.9	4.8	9.1	3.9	8.9	4.3	5.6	2.6
C20:5ω3	—	7.9	—	—	—	—	2.3	—	—	—	—	—	—	—	1.8	—	—	—
C22:3ω3	—	—	2.5	—	2.3	—	—	—	—	—	—	—	—	—	—	—	—	—
C22:5ω3	—	1.8	—	—	—	—	3.4	—	2.2	—	—	—	—	—	—	—	—	—
C22:6ω3	—	32.5	—	—	—	—	3.9	—	1.9	—	7.9	3.7	7.9	3.2	11.6	5.2	8.9	4.0
% lipid, g/100 g tissue	—	—	0.88	1.87	0.92	2.12	0.95	1.86	1.40	3.01	1.22	2.12	1.02	2.29	0.92	1.97	1.17	3.03

[1]Fatty acids in amounts of 2% or less omitted. B = Breast meat; T = thigh meat.
[2]All groups of turkeys were fed a basal diet plus an oil supplement for 6 wk. Group 1 = 4% safflower oil (SO), Group 2 = (same as 1) + 125 ppm ethoxyquin (EMQ), Group 3 = 1% SO + 3% linseed oil (LO), Group 4 = (same as 3) + 125 ppm EMQ, Group 5 = 3.5% SO + 0.5% tuna oil (TO), Group 6 = (same as 5) + 125 ppm EMQ, Group 7 = 3% SO + 1% TO, Group 8 = (same as 7) + 125 ppm EMQ.

TABLE 2.—Taste panel scores (rank) on breast and thigh meat and skin of turkeys fed to 6 wk of age diets containing varying levels of safflower oil, linseed oil, and tuna fish oil with and without ethoxyquin.

Group[1]	Breast meat	Thigh meat	Skin
	Odor[2]		
	Without antioxidant		
1, 4% SO	1.9	2.4	2.9
3, 3% LO	2.4	3.0	2.6
5, 0.5% TO	2.5	1.9	2.3
7, 1% TO	3.2	2.8	2.4
	With antioxidant		
2, 4% SO	1.9	2.2	2.5
4, 3% LO	2.6	2.2	2.7
6, 0.5% TO	2.1	2.4	2.2
8, 1% TO	3.5	2.9	2.7
	Flavor[2]		
	Without antioxidant		
1, 4% SO	1.9	2.3	2.5
3, 3% LO	2.4	[3]3.2 (4F)	[3]3.0 (1F)
5, 0.5% TO	2.7	2.1	1.9
7, 1% TO	3.0	[3]2.4 (1F)	[3]2.6 (1F)
	With antioxidant		
2, 4% SO	2.3	1.9	2.6
4, 3% LO	2.3	2.3	2.9
6, 0.5% TO	2.1	2.4	2.1
8, 1% TO	[3]3.3 (2F)	[3]3.3 (1F)	2.5

[1]All groups of turkeys were fed a basal diet plus an oil supplement for 6 wk. Group 1 = 4% safflower oil (SO), Group 2 = (same as 1) + 125 ppm ethoxyquin (EMQ), Group 3 = 1% SO + 3% linseed oil (LO), Group 4 = (same as 3) + 125 ppm EMQ, Group 5 = 3.5% SO + 0.5% tuna oil (TO), Group 6 = (same as 5) + 125 ppm EMQ, Group 7 = 3% SO + 1% TO, Group 8 = (same as 7) + 125 ppm EMQ.
[2]Rank 1 = least off odor or off flavor.
[3]F = number of fishiness comments.

iment (Miller and Robish, 1969; Dreosti, 1970; Opstvedt, Nygard, and Olsen, 1970).

Some suggestions may be offered as to why no clear fishy flavors were induced, even though there was uptake of linolenates in the turkey carcass. For example, the use of safflower oil to achieve lipid isocaloric balance may have depressed the uptake of linolenates. Edwards and May (1965) observed this effect when they fed mixtures of corn and menhaden oil. Certainly the metabolism of the young birds (in this experiment 6 wk of age) must be considered. Their cell turnover is considerably higher than that of adult birds; phospholipid (an integral part of cell membranes) turnover is proportional to mitotic rate, and long-chained fatty acids are more readily found in phospholipids.

Experiment II

As before, all turkeys appeared to be in good nutritional health. The mean dressed weight was 1,377 g for turkeys fed to 8 wk of age.

Table 3 shows the results of fatty acid (methyl esters) determination by GLC of lipids extracted from the breast of turkeys fed fish oil and safflower oil to 8 wk of age. The fatty acids C20:5ω3 and

TABLE 3.—Methyl ester fatty acid composition of tuna oil and lipids extracted from the breast of turkeys[1] fed to 8 wk of age diets containing varying levels of tuna oil and beef fat or safflower oil with and without vitamin E (*dl*-α-tocopherol acetate) supplementation.

Fatty acid	Tuna oil[2]	% distribution in extracted oil							
		Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7	Group 8
C14	3.1	0.7	1.0	0.7	0.5	0.4	0.5	0.3	0.5
C14:1	—	0.2	0.2	0.1	0.1	0.1	0.1	0.0	0.1
C15	—	0.2	0.2	0.2	0.2	0.3	0.2	0.1	0.2
Iso C16	—	3.3	3.3	3.1	3.5	3.9	3.7	2.6	3.3
C16	—	14.8	14.3	14.3	13.7	14.5	14.3	15.2	14.9
C16:1	4.7	1.1	1.2	0.9	0.6	0.6	0.9	0.3	0.6
C17	—	0.5	0.6	0.5	0.6	0.8	0.7	0.7	0.7
Iso C18	—	1.7	1.4	1.4	2.1	1.3	1.6	0.7	0.9
C18	5.5	15.4	14.9	15.0	15.3	14.9	14.6	13.6	11.2
C18:1	15.8	20.8	18.9	17.4	15.7	14.7	14.9	11.1	12.8
C18:2	4.8	24.8	20.6	19.9	18.5	18.0	18.1	30.9	28.9
C18:3	—	0.8	0.7	0.5	0.3	0.5	0.5	0.5	0.7
C20:4	3.0	6.6	5.9	6.5	7.4	6.2	6.4	8.8	6.5
C20:5	7.9	0.7	2.4	3.3	3.4	4.2	4.3	1.8	3.3
C22:5	1.8	1.2	1.6	1.5	1.6	2.0	1.5	1.0	1.0
C22:6	32.5	3.3	10.3	11.9	13.4	14.9	15.5	9.2	11.8
Others	21.0	3.9	2.5	2.8	3.1	2.7	2.2	3.2	2.6
% lipid, g/100 g tissue	—	0.89	0.95	0.98	0.86	0.84	0.90	0.93	0.84

[1]All groups of turkey were fed a basal diet plus an oil supplement for 8 wk. Group 1 = 4% beef fat (BF), Group 2 = 3.5% BF + 0.5% tuna oil (TO), Group 3 = 3% BF + 1% TO, Group 4 = (same as 3) + 200 mg/kg vitamin E, Group 5 = 2% BF + 2% TO, Group 6 = (same as 5) + 200 mg/kg vitamin E, Group 7 = 3% safflower oil (SO) + 1% TO, Group 8 = 2% SO + 2% TO.

TABLE 4.—Methyl ester fatty acid composition of lipids extracted from the cooked breast of turkeys[1] fed to 8 wk of age diets containing varying levels of beef fat and tuna oil with and without vitamin E (*dl*-α-tocopherol acetate) supplementation.

Fatty acid	% distribution in extracted oil		
	Group 1	Group 5	Group 6
C14	0.8	1.1	0.9
C14:1	0.1	0.3	0.2
C15	0.2	0.3	0.3
Iso C16	2.7	2.3	1.8
C16	15.9	16.6	15.9
C16:1	0.8	2.2	1.7
C17	0.6	0.9	0.8
Iso C18	1.6	1.4	1.1
C18	17.1	14.1	14.5
C18:1	19.1	21.2	18.8
C18:2	22.5	19.3	19.7
C18:3	0.6	0.9	0.8
C20:4	5.1	3.4	4.7
C20:5	1.8	2.5	3.1
C22:5	1.0	1.1	1.1
C22:6	6.6	9.2	11.5
% lipid, g/100 g tissue	1.10	1.15	1.10

[1]All groups of turkeys were fed a basal diet plus an oil supplement for 8 wk. Group 1 = 4% beef fat (BF), Group 5 = 2% BF + 2% tuna oil, Group 6 = (same as 5) + 200 mg α-tocopherol acetate per kilogram.

C22:6ω3 increase as the amount of tuna oil increases in the diet. Safflower oil added to Diets 7 and 8 seemed to reduce the uptake of these fatty acids. Tocopherol acetate supplementation did not seem to have any effect on the uptake of ω3 fatty acids. Fatty acid distribution analyses (Table 4) on lipids extracted from cooked turkey breast from Groups 1, 5, and 6 show that α-tocopherol did not have an effect on the relative stability of the long-chain fatty acids during cooking.

The results of taste panel evaluations (Table 5) show that, while α-tocopherol supplementation did not change the ω3 fatty acid distribution, it greatly reduced fishy flavor as judged by the taste panel. Opstvedt, Nyard, and Olsen (1970) also reported these findings. On the other hand, safflower oil (used to achieve isocaloric balance) reduced the uptake of ω3 fatty acids, but there were no differences in flavor when compared to the flavor of turkeys fed the same amount of tuna oil but using beef fat for isocaloric balance. There was a strong relationship between the amount of C20:5ω3 and/or C22:6ω3 and fishy flavor when no α-tocopherol or safflower oil supplementation was present in the diets. This agrees with the findings of Neudoerffer and Lea (1966, 1967), Miller et al. (1967a), Miller and Robish (1969), and Dreosti (1970). However, a comparison of the fatty acid distributions and lipid contents found by these investigators with those in this experiment and Experiment I, shows that the levels of C20:5ω3 and C22:6ω3 present when fishy flavors are detected are higher in these experiments. We should also note that the fish oils used by other investigators contained about 2-12% C22:6ω3, while the tuna oil used in these experiments contained 32% C22:6ω3.

Experiment III

These 16-wk-old turkeys had been fed diets containing 3% beef fat plus 1% tuna oil and 2% beef fat plus 2% tuna oil for the 2 wk prior to slaughter. The control diet contained 4% beef fat. All turkeys apparently enjoyed good nutritional health and the mean dressed weight was 3,585 g.

TABLE 5.—Mean[1] taste panel scores[2] and Duncan's multiple range test of mean scores on thigh and breast meat and skin of turkeys fed to 8 wk of age diets containing varying levels of tuna fish oil and beef fat or safflower oil with and without vitamin E (*dl* α-tocopherol acetate) supplementation.

Group[3]	Breast meat	Group[3]	Thigh meat	Group[3]	Skin
5, 2% TO + 2% BF	3.91	8, 2% TO + 2% SO	3.56	8, 2% TO + 2% SO	3.37
8, 2% TO + 2% SO	3.35	5, 2% TO + 2% BF	3.28	5, 2% TO + 2% BF	2.69
3, 1% TO + 3% BF	3.04	6, 2% TO + 2% BF + E	2.41	3, 1% TO + 3% BF	1.99
2, 0.5% TO + 3.5% BF	2.94	2, 0.5% TO + 3.5% BF	2.20	6, 2% TO + 2% BF + E	1.98
6, 2% TO + 2% BF + E	2.48	7, 1% TO + 3% SO	2.03	7, 1% TO + 3% SO	1.69
7, 1% TO + 3% SO	2.30	3, 1% TO + 3% BF	1.85	1, 4% BF	1.27
1, 4% BF	1.33	4, 1% TO + 3% BF + E	1.22	2, 0.5% TO + 3.5% BF	1.26
4, 1% TO + 3% BF + E	1.24	1, 4% BF	0.95	4, 1% TO + 3% BF + E	1.04
$S_{\bar{x}}$	0.228		0.211		0.252

[1]Means connected by a common line are not significantly different at the 0.05 probability level.
[2]1 = no fishy flavor, 5 = very fishy.
[3]All groups of turkeys were fed a basal diet plus an oil supplement for 8 wk. Group 1 = 4% beef fat (BF), Group 2 = 0.5% tuna oil (TO) + 3.5% BF, Group 3 = 1% TO + 3% BF, Group 4 = (same as 3) + 200 mg/kg vitamin E (E) Group 5 = 2% TO + 2% BF, Group 6 = (same as 5) + 200 mg/kg vitamin E, Group 7 = 1% TO + 3% safflower oil (SO), Group 8 = 2% TO + 2% SO.

TABLE 6.—Methyl ester fatty acid composition of lipids extracted from the thighs of turkeys[1] fed from 14 wk to 16 wk of age diets containing varying levels of beef fat and tuna oil.

Fatty acid	% distribution in extracted oil		
	Group A	Group B	Group C
C14	0.4	1.0	1.0
C14:1	0.1	0.1	0.1
C15	0.1	0.2	0.2
Iso C16	1.9	2.1	1.6
C16	17.7	16.8	18.7
C16:1	5.8	1.8	1.9
C17	0.3	0.5	0.6
Iso C18	0.9	0.8	0.7
C18	10.6	13.8	12.1
C18:1	21.7	20.3	20.4
C18:2	30.7	26.4	26.2
C18:3	1.6	1.3	1.5
C20:4	5.2	6.2	5.0
C20:5	0.2	0.9	1.4
C22:5	0.5	0.8	0.7
C22:6	0.5	4.5	6.1
% lipid, g/100 g tissue	2.10	2.12	2.55

[1]All turkeys were fed a basal diet without oil supplement to 14 wk of age and to 16 wk of age with oil. Group A = 4% beef fat, Group B = 3% beef fat + 1% tuna oil, Group C = 2% beef fat + 2% tuna oil.

Fatty acid distributions and percent extracted lipids from the thighs of these turkeys are shown in Table 6. (The same analyses were not possible for the breast meat because it was used in another experiment.) As before, the amount of C22:6ω3 increased as the amount of fish oil in the diet increased. It is of interest that the lipid level was only slightly higher in the 16-wk turkeys fed fish oil for 2 wk than in the 6- or 8-wk turkeys fed from day 4 to slaughter. Yet, the percent of C22:6ω3 was less than half that of the 8-wk birds, while the flavor reported in Table 7 was at least as fishy, if not more so.

In conclusion, if consideration is given to 1) the effects of α-tocopherol on (reducing) the fishy flavor, while not affecting the uptake of linolenates, and 2) the different levels of long-chain linolenates present when fishiness is detected, one has to reason that the long-chained ω3 fatty acids do not of themselves cause fishy flavor by their simple presence. It is plausible that the fishy flavors result at least in part from the oxidation (in vivo? postmortem?) of linolenates and that α-tocopherol limits the oxidation. It is further colorable that the amount of linolenate oxidation needed to produce fishy flavor may be smaller than the inherent error in fatty acid analyses and therefore, no differences would be observed in the amount of linolenates in the carcass of turkeys fed fish oils with and without α-tocopherol.

TABLE 7.—Mean taste panel scores[1] and regression equations (% tuna fish oil supplement vs. mean taste panel scores) for thigh and breast meat and skin of turkeys fed diets containing varying amounts of beef fat and tuna oil.

Group[2]	Breast meat	Thigh meat	Skin
A, control	1.44	1.11	1.06
B, 1 TO	2.06	2.50	1.89
C, 2 TO	3.28	4.11	2.94
$S_{\bar{x}}$	0.26	0.21	0.28
Regression equations:			
$y = 1.343 + 0.917X$			
$y = 1.074 + 1.500X$			
$y = 1.018 + 0.944X$			

[1] = no fishy flavor, 5 = very fishy.
[2]All groups of turkeys were fed a basal diet without oil supplementation to 14 wk of age and to 16 wk with oil. Group A = 4% beef fat, Group B = 3% beef fat + 1% tuna oil (TO), Group C = 2% beef fat + 2% TO.

ACKNOWLEDGMENT

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ZOOGEOGRAPHY OF THE GENUS *NEMATOSCELIS* (CRUSTACEA, EUPHAUSIACEA)

K. GOPALAKRISHNAN[1]

ABSTRACT

The International Indian Ocean Expedition provided zooplankton samples to study the distribution and seasonal changes in numerical abundance of *Nematoscelis* in the Indian Ocean. Distributional boundaries of species of this genus in the Atlantic and Pacific oceans were determined mainly on the basis of mid-water trawls. All seven species of this genus occur in the Pacific, whereas only five species are present in the Indian and four in the Atlantic. Two forms ("old" and "new") of *N. gracilis*, considered to be ecophenotypes, but distinguished on the basis of morphological differences observed in the petasma, occupy the tropical Indo-Pacific subregion. The "old form" is most abundant in the oxygen-poor waters of the Arabian Sea, Bay of Bengal, and also in the eastern tropical Pacific. The "new form" is mostly confined to areas of the South Equatorial Current. The present study indicates that *N. gracilis* does not occupy the equatorial zone of the Atlantic Ocean, but "new forms" are transported from the Indian Ocean up to the southern tip of South Africa. *Nematoscelis atlantica* is distributed in the central water masses of the Pacific and Indian oceans, whereas in the Atlantic its distribution extends also to the equatorial zone. *Nematoscelis microps* and *N. tenalla* are warmwater species and are distributed between lat. 40°N and 40°S, although lacking in most areas of low oxygen water. *Nematoscelis lobata* has restricted distribution in the region of the Philippines. *Nematoscelis megalops* occupies the circumpolar transitional regions of the Southern Hemisphere and also the subarctic and transition subregions of the North Atlantic. *Nematoscelis difficilis* is endemic to the North Pacific transition zone. The basins of Timor and Banda Seas and their associated straits in the Indo-Australian Archipelago appear to allow inter-ocean gene flow among populations of *N. gracilis*, *N. Microps*, and *N. tenella*. A similar communication exists between Atlantic and Indian Ocean populations of these species through the oceanic waters around the tip of South Africa.

Zoogeography of the order Euphausiacea is reasonably well known for the Pacific Ocean (Brinton, 1962). The study on the distribution of euphausiids in the Indian Ocean is still in its preliminary phase. Available data from this ocean are adequate to make possible estimates of species ranges only. The role of the biological program during the International Indian Ocean Expedition (IIOE) (1960-65) was to provide materials from wide areas of the ocean to facilitate a better understanding of distributions of many zooplankton taxa in the Indian Ocean. Therefore, in the present study it was decided to put more effort into understanding the geographical distribution and seasonal abundance of Indian Ocean species of *Nematoscelis* than those from the Pacific and Atlantic oceans. Preliminary observations on the distribution of Euphausiacea as a whole were made by Gopalakrishnan and Brinton (1969). Subsequently, Brinton and Gopalakrishnan (1973) brought the distributional information up to date on the basis of IIOE samples studied up to that time.

Ocean-wide records of species of euphausiids in the Indian Ocean come from three major expeditions: the Percy Sladen Trust Expedition (Tattersall, 1912), the Deutsche Tiefsee Expedition (Illig, 1930), and the John Murray Expedition (Tattersall, 1939). Studies on the regional fauna are available for the eastern waters of South Africa (Boden, 1951), Red Sea, Arabian Sea, and Bay of Bengal (Ponomareva, 1964, 1968). Species of *Nematoscelis* of the southwest coast of India were provided by Sebastian (1966). Only four of the seven species of this genus have been reported from the Indian Ocean: *N. gracilis*, *N. megalops*, *N. microps*, and *N. tenella*. The present study confirms the presence of a fifth species, *N. atlantica*, in the southern Indian Ocean. *Nematoscelis megalops* was described by Boden (1951) from the southern African waters. Three females of this species were reported by Illig (1930) from southwest of Ceylon in the northern Indian Ocean. The present investigation does not confirm its distributional range in that region.

Nematoscelis difficilis is an endemic species of

[1]Scripps Institution of Oceanography, La Jolla, CA 92037; present address: The Hawaii Institute of Marine Biology, University of Hawaii, P.O. Box 1346, Kaneohe, HI 96744.

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the transition zone in the North Pacific and is not reported from anywhere else. Previous studies on the distribution of all seven species of *Nematoscelis* in the Pacific Ocean are summarized by Brinton (1962).

Only four species of *Nematoscelis* have been reported from the Atlantic Ocean. Moore (1952) studied ocean-wide distributions of many euphausiids in the North Atlantic Ocean, including *N. microps* and *N. megalops*. Einarsson (1945) also reported *N. megalops* from the northeastern Atlantic. From the Mediterranean Sea *N. megalops, N. microps,* and *N. atlantica* were reported by Ruud (1936) and Casanova-Soulier (1968). Incorporating all previous records Mauchline and Fisher (1969) have provided a generalized picture of the distribution of *Nematoscelis* in the Atlantic Ocean. Gopalakrishnan (1973) examined the pattern of vertical distribution of *Nematoscelis* species of the Pacific Ocean.

METHODS AND MATERIALS

The Indian Ocean portion of the present study of *Nematoscelis* is based on samples collected during the IIOE. This expedition was a collaborative venture in which 10 countries participated and 16 vessels collected zooplankton samples as part of the biological program during 1960-65. The composite pattern of stations occupied during 70 cruises provided coverage of most geographical provinces of the Indian Ocean (Figure 1a, b). A standard procedure was followed by all participating vessels for collecting zooplankton samples. Accordingly, each sample was obtained by using the Indian Ocean Standard Net (IOSN) which was specially devised for the IIOE (Currie, 1963). It is a ring net with a mouth area of 1 m^2 and a length of 5 m. The straining surface is nylon gauze of 0.33-mm mesh. Hauls were as nearly vertical as possible, from approximately 200-m depth to the

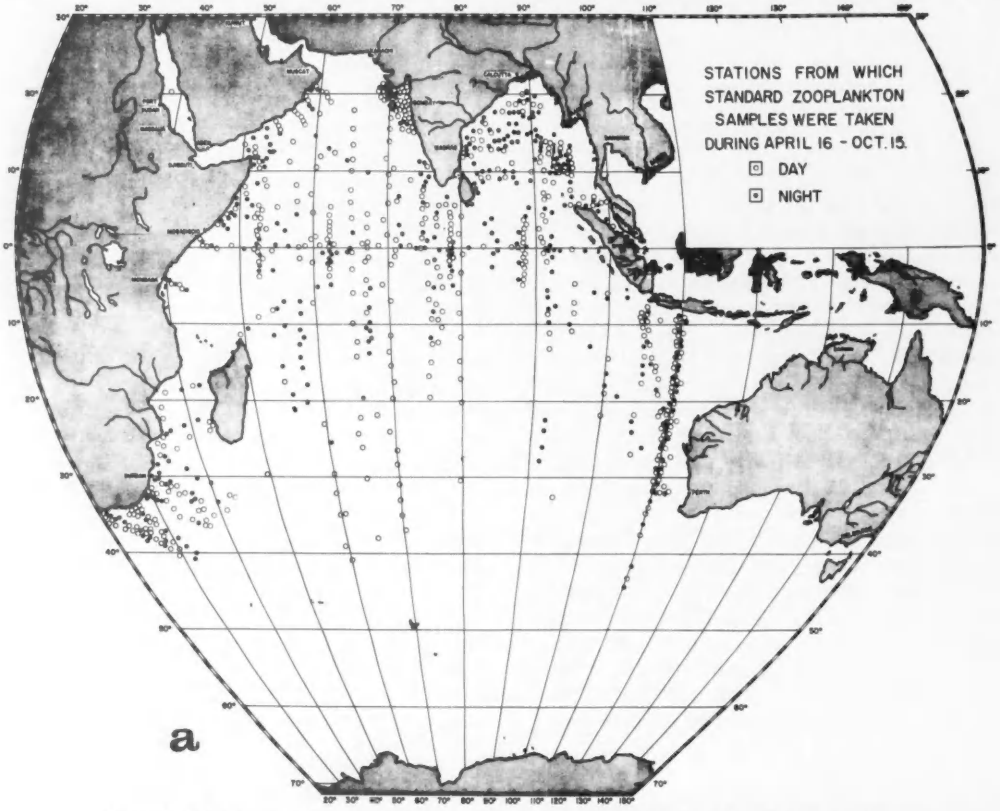

FIGURE 1.—Plankton samples examined for *Nematoscelis* of the Indian Ocean: a - SW Monsoon period.

surface. Assuming 0° wire angle the net would be expected to filter approximately 200 m^3 of water; but 0° wire angle was rarely attained at sea. Moreover, Tranter and Smith (1968) showed that the initial filtering efficiency of this net is 0.96; subsequent clogging does not reduce the filtering volume significantly.

Plankton samples collected according to these procedures are classified as "standard." In waters over the continental shelf where the depth was less than 200 m, the net was usually hauled up from within a few meters of the bottom; such collections were also treated as standard since the full water column was filtered. Samples collected from less than approximately 200-m depth in the open ocean, where the depth was far greater than 200 m, were designated as "nonstandard."

All samples were processed and sorted at the Indian Ocean Biological Centre situated in Cochin, India. The list of plankton samples processed at this center is included in a handbook to the international collections (Indian Ocean Biological Centre, 1969). The locality, time, and depth of haul at each station are given in this list, along with total displacement volume of the sample and fraction of each sample that was sorted into major taxa. At the sorting center a 3- to 4-ml portion of each sample was sorted into its constituent major taxa after removing large individuals from the sample. Individuals in each group were then counted to give an estimate of numbers in the whole sample. The sorted fractions ranged from 5% to 90% of the whole sample on the basis of the initial displacement volume of the sample. Further details of the sorting procedure were described by Hansen (1966). The unsorted portion (archive) of all samples were deposited at the Indian Ocean Biological Centre. About 215 of them were examined during the present study in order to check whether the fractionating proce-

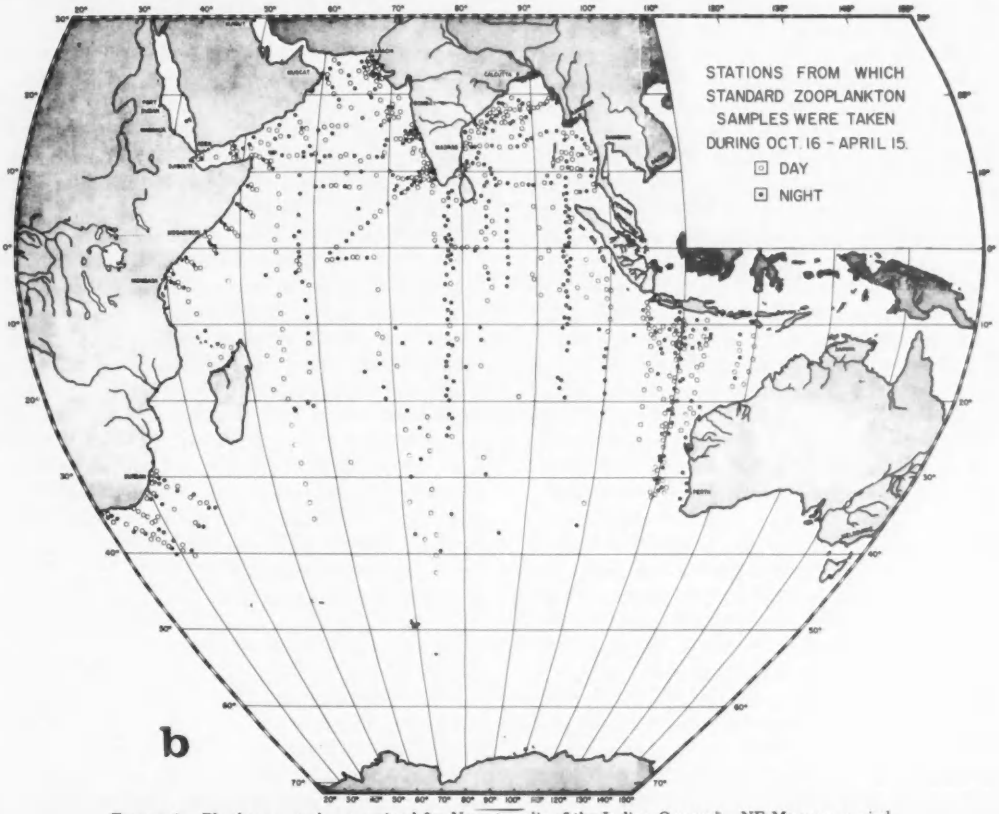

FIGURE 1.—Plankton samples examined for *Nematoscelis* of the Indian Ocean: b - NE Monsoon period.

dure was efficient enough to retain all species of *Nematoscelis* present in the whole sample. Only 26 archives were found to have contained one or more species not present in their subsamples. Therefore it is assumed that the subsampling procedure was usually adequate.

The wind system over the Indian Ocean is monsoonal. The two monsoon phases are designated as the Southwest (SW) and Northeast (NE) monsoons, indicating the predominant wind directions in the northern Indian Ocean during each phase. The bulk of the samples were grouped into two categories: those collected during 16 April to 15 October falling in the SW monsoon and those collected during 16 October to 15 April falling in the NE monsoon. The period 16 April to 15 October generally agrees with that of the wind regime of the SW monsoon (Wooster, Schaefer, and Robinson, 1967).

Of the 1,927 samples processed at the Indian Ocean Biological Centre, 1,732 samples were examined for the study of *Nematoscelis*. Of these, 879 samples were taken during the SW monsoon and 853 during the NE monsoon. Since a comparison of day and night catches of total euphausiids showed differences in day and night estimates (Gopalakrishnan and Brinton, 1969), it was decided to group day and night counts separately for each season. There were 401 night and 478 day samples for the SW monsoon period and 413 night and 440 day samples for the NE monsoon.

In order to fill gaps in certain geographical areas, some samples collected by using gear other than the IOSN have also been used in the preparation of charts. *Kistna* cruises 2 to 6 used an organdy net with 50-cm mouth diameter. *Natal* cruises 1 and 4 used the N-70 net with 70-cm mouth diameter. These samples were standardized for comparing with IOSN samples: the organdy net samples were multiplied by a factor of 5.1 and N-70 net samples by a factor of 2.6. In addition to these samples, 26 nonstandard surface samples taken during the *Patanela* cruise were also examined for qualitative information. *Argo* Monsoon Expedition stations 9-27 (ref. Snyder and Fleminger, 1972) have also been used in the preparation of present charts. These samples were collected using 1-m nets.

The observed differences between day and night catches of adult euphausiids are due to the fact that during day time many species either migrate to deeper layers or are able to dodge the net. Total euphausiids were 1.5-2.0 times more abundant in night samples than in day samples (Gopalakrishnan and Brinton, 1969). The mouth area of the IOSN is only 1 m^2 and it is probable that many large zooplankters can avoid the net. However, most samples taken at night contained many adult euphausiids, including some of the large thysanopods that migrated into the upper layer. All species of *Nematoscelis* are smaller than most *Thysanopoda* species. It is reasonable to believe that the IOSN tows taken at night would have been adequate to representatively sample adult species of *Nematoscelis*.

The present distributional study of *Nematoscelis* in the Indian Ocean is limited to the upper 200 m only. The geographical distribution of each species of this genus is compared with the pattern of water circulation in the upper layer. Larvae and juveniles of all *Nematoscelis* species are confined to the upper 200-m layer during both day and night, whereas adults undertake diurnal vertical migration (Gopalakrishnan, 1973). During daytime the distribution of adults extends from the upper 200-m layer to about 600-800 m; but at night, because of their upward migration, the range extends from the surface to about 400-600 m only, with the maximum above 200 m in most geographical regions. It is therefore probable that the IOSN would have caught adults better at night than during the day. For this reason only night samples were considered in charting the distribution of adults. However, a few trawls (Isaacs-Kidd Mid-water trawl) fished from depths greater than 200 m, were also used for examining overall geographical range. Station positions of these are included in Figures 7, 11, and 18. Most of these reached as deep as ca. 900-1,000 m, somewhat deeper than the lower limit of the vertical range of *Nematoscelis*. The geographical coverage of these trawls was not sufficient to examine the influence of deep circulation on the distribution of species. A total of 286 mid-water trawl samples were examined from the Pacific, Atlantic, and Indian oceans. [Collections from the Pacific and Indian oceans are located at the Scripps Institution of Oceanography. Collecting data regarding many of these appear in Clarke (1963).] The approximate boundaries of distribution of each species are shown on the basis of present evidence, including literature records.

The distributional ranges of species of *Nematoscelis* in the Atlantic Ocean were based on specimens sorted from fractions of plankton samples obtained by the Woods Hole Oceanographic

Institution. Most of the samples were from the North Atlantic. Charts were prepared for each species of *Nematoscelis*; but the abundance is expressed only as the percentage of the total *Nematoscelis* present in the aliquot, because the aliquot itself was an unknown quantitative fraction of the whole sample. *Atlantis II* and *Chain* cruises took samples using a 75-cm net from above 100 m; *Delaware* samples were also taken from similar depths, but by using 1-m nets. Lusiad VII cruise in the South Atlantic collected samples from 200 m to surface. In all, 217 plankton samples were examined from the Atlantic Ocean.

HYDROGRAPHY OF THE INDIAN OCEAN

In the upper strata of the sea, the general circulation may be related to the prevailing wind system. This wind-driven oceanic circulation affects and modifies the distribution of water masses in the upper strata; the wind-driven circulation penetrates into deeper layers and can be recognized at intermediate depths (Reid, 1965). The thermohaline circulation, caused by density differences in the ocean due to heat and water exchanges with the atmosphere, is thought to be responsible for formations of deepwater masses and the deep circulation (Neumann and Pierson, 1966). As a result of these types of circulations, properties such as temperature, salinity, oxygen, and nutrients show distinct features in their distributions in different oceanic areas, providing different characteristic habitat conditions for individual species or communities of organisms.

Since a major part of the present study deals with the seasonal distributions of Indian Ocean species of *Nematoscelis*, it is pertinent to provide a general background of the available information on the monsoonal seasons prevailing over the Indian Ocean. The surface currents of the Indian Ocean during the monsoon periods are described by Taft (1971) and for the present study I will follow his discussion of the wind and current patterns (see Neumann and Pierson, 1966, and Taft, 1971, for illustrations of surface currents of the Indian Ocean). Hydrographical changes associated with the monsoon are well documented for the Arabian Sea (Wooster et al., 1967). During the NE monsoon the northeast winds of the Northern Hemisphere cross the Equator into the Southern Hemisphere, there becoming northwesterly. This monsoon phase is established in November and persists through March; its maximum intensity is in January. During this phase a broad doldrum belt develops at about lat. 5°S to lat. 10°S between weak northerly winds and the southeast trade winds. In the SW monsoon, southeast trades from the Southern Hemisphere cross the Equator and gradually turn into southerly and southwesterly directions in the Northern Hemisphere. Winds are especially intense during this period near the African, Somali, and Arabian coasts. The SW monsoon is well established in May and persists through September. It is most intense in July.

The onset of monsoon periods in the Indian Ocean is found to be symmetrical in time (Wooster et al., 1967; Taft, 1971). Each period lasts for 5 mo; April and October are transition periods. Because of these short periods of transition in the monsoon system, it was decided to divide each April and October period into two halves and add the first half of April and the latter half of October to NE monsoon. The latter half of April and the first half of October were similarly added to the SW monsoon period. The overall winds and surface currents are far stronger in the SW monsoon than in the NE mqnsoon.

The surface circulation plays an important role in the distribution of planktonic animals in the ocean. In the Indian Ocean the surface circulation is subjected to a longer seasonal change than in other oceans. The outstanding features of the surface circulation are: 1) currents that follow in a more or less zonal direction far from the continents, and 2) currents near continental coasts. During the NE monsoon the North Equatorial and the South Equatorial currents flow westward and the Equatorial Countercurrent flows eastward between these two currents. Unlike those in the Pacific and Atlantic, the countercurrent in the Indian Ocean is situated in the Southern Hemisphere. This is related to the position of the doldrums south of the Equator. The South Equatorial Current, after reaching the African coast, contributes water to the Agulhas Current flowing southwest and also to the eastward flowing Countercurrent. During the NE monsoon the Somali Current, flowing southwest with a speed of about 100 cm/s, merges into the Mozambique Current (Neumann and Pierson, 1966), thereby bringing many tropical species as far south as lat. 35°-40°S along the coast of Africa. At this time the surface current off the southwest coast of India is also weak and flows in a southeast direction. In the Bay

of Bengal the general circulation is counterclockwise. Unlike in the Pacific and Atlantic oceans, there is little evidence of an eastern boundary current in the Indian Ocean along the west coast of Australia. According to Wyrtki (1973), water movements in this region are weak and variable and most of the northward flow is situated farther offshore between long. 95°E and 105°E. In the Indian Ocean the Equatorial Undercurrent is also seasonal, being more pronounced during the NE monsoon than in the opposite season (Taft and Knauss, 1967; Taft, 1971).

At the onset of the SW monsoon the surface currents in the Indian Ocean change dramatically. The westward flowing North Equatorial Current is replaced by an eastward flowing Southwest Monsoon Current, thereby reversing the surface circulation in that region. Together with the Somali Current it is the outstanding current in these latitudes. The surface current north of lat. 5°S is then directed eastward and the Equatorial Countercurrent is not distinguishable as a separate flow. This is contrary to the conditions prevailing in other oceans where the intensity of the Countercurrent reaches a maximum during this period. The Somali Current, now flowing northeast as an intense western boundary current, extends to about lat. 8°N. The current transports southern forms into the Arabian Sea thereby serving to increase the faunal complexity of the region. In addition, enrichment of surface water north of the current produces zooplankton blooms. North of lat. 8°N the data suggest that this current leaves the coast and turns eastward (Taft, 1971). The South Equatorial Current becomes intensified in the western Indian Ocean; near the African coast it contributes to part of the northern flow. This brings species of the southern latitudes close to the Equator in the western Indian Ocean and even occasionally farther north to about lat. 10°N along the western boundary. During the SW monsoon the flow off the Arabian coast is toward the east and northeast but is much less intense than the Somali Current. This flow starts in April and is reported to persist until August. The southeastward flow off the southwest coast of India remains the same as in the NE monsoon. In this region the current flows northward only for 2 mo and it is essentially opposite to the prevailing wind stress. Taft (1971) pointed out that the circulation in the eastern Arabian Sea is therefore influenced by thermohaline processes.

During the SW monsoon three areas are prominent in the Arabian Sea for upwelling: off the Somali, Arabian, and southwest Indian coasts. There is evidence that the upwelling off the Arabian coast is wind driven; that off the Somali coast is partly wind driven and partly due to dynamic constraint on the current (Taft, 1971); and that off the coast of southwest India is due to the dynamic response which involves tilting of the thermocline up toward the coast (Darbyshire, 1967; Banse, 1968). The cool surface waters off the coasts of Arabia and Somalia during the SW monsoon are clear indication of intense upwelling (See Wyrtki, 1971:45). Along the western Indian Ocean Düing (1971) commented on the presence of many offshore anticyclonic and cyclonic vortices which are indicated by alternating highs and lows of dynamic height persisting through both monsoon phases. Taft (1971) singled out the importance of these vortices in the mixing processes of the near-surface waters which would increase the rate of nutrient enrichment of the surface layer. In the western Arabian Sea such enrichments are maximum during the June-August period (Table 1). High values of NO_3-N and SiO_3-Si persist for a longer period along the coast of Somalia than off the Arabian coast. The plankton atlas of the IIOE (Indian Ocean Biological Centre, 1968) shows that the maximum abundance of zooplankton is also associated with these upwelling areas.

The distribution of surface temperature during the NE monsoon indicates no cool surface water in

TABLE 1.—Surface nutrients at four coastal regions of the Arabian Sea. A = off the coast of Arabia, lat. 20°N; B = off the coast of India, lat. 20°N; C = off the coast of Somalia, lat. 10°N; D = off the coast of southwest India, lat. 10°N. All values are in μg-at/l. (Data from Wooster et al., 1967.)

	Dec.-Feb.				Mar.-May				June-Aug.				Sept.-Nov.			
Nutrients	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
PO_4-P	0.75	0.25	0.25	0.50	>0.25	0.25	0.25	0.25	>2.0	0.50	1.0	>0.25	>1.0	>0.25	1.0	0.25
NO_3-N	all values <2.5				all values <2.5				>25.0	2.50	>15.0	<2.5	<2.5	<2.5	15.0	<2.5
SiO_3-Si	all values 5.0				all values <5.0				>20.0	<5.0	>20.0	<5.0	10.0	<5.0	>15.0	<5.0

the Arabian Sea (see Wyrtki, 1971:38). Isotherms slope southwestward toward the African coast. During this period no upwelling is observed off the southwest coast of India, although the Ekman theory would predict upwelling in this area since the surface winds blow equatorward and parallel the coast. Taft (1971) suggested that this may be due to the low speed of the northeasterly wind.

In the Bay of Bengal upwelling has been reported to occur seasonally along the east coast of India and west coast of Burma (La Fond, 1954, 1957; Banse, 1960; La Fond and La Fond, 1968). During the early part of the NE monsoon, the northeasterly winds displace subsurface water offshore along the Burmese coast. Wyrtki (1961) also reported upwelling along the coast of Burma and Thailand during the December-February period. The general surface circulation of the Bay of Bengal is clockwise during January through July and it becomes counterclockwise from August to December (La Fond and La Fond, 1968). The southwesterly winds prevail over the northern Bay of Bengal in March and over the entire region in April. During these months an intense upwelling is noticed along the east coast of India (La Fond and La Fond, 1968). In this region, along with the nearshore occurrence of dense water, the average sea level also reaches a minimum height during this period (La Fond, 1954).

A remarkable feature of the Indian Ocean is the rapid attenuation of dissolved oxygen with depth; at 200 m values become 0.2 ml/l or less in the Arabian Sea and Bay of Bengal (Wyrtki, 1971). Vinogradov and Voronina (1961) and Vinogradov (1968) have discussed the association of low zooplankton biomass within the oxygen minimum layer in the Arabian Sea. North-south and east-west transects in the Arabian Sea indicate that oxygen values as low as 0.1 ml/l occur below 200 m during both seasons (Figure 2A, B). According to Wyrtki (1971) the concentrations of oxygen in the minumum layer do not vary seasonally, although the depth of this layer changes. The vertical profile at four north-south transects across the equatorial Indian Ocean show the occurrence of very low oxygen concentrations below 100 m (Figure 3). Since these profiles were taken during different months, it appears that this feature persists throughout the year.

The vertical distribution of temperature along four north-south transects (same transects as shown in Figure 3) indicates that the thermocline is situated between 75 and 100 m in the regions north of lat. 10°S. The South Equatorial Current

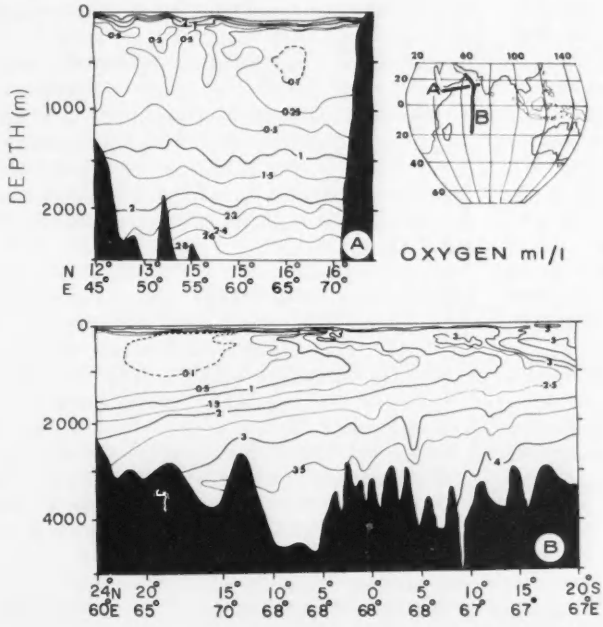

FIGURE 2.—Vertical distribution of oxygen in the Arabian Sea: A. East-west transect along lat. 11°N, long. 45°E to lat. 16°S, long. 72°E (July-August); B. North-south transect along lat. 24°N, long. 60°E to lat. 20°S, long. 67°E (November-May). (Charts reproduced from Wyrtki, 1971.)

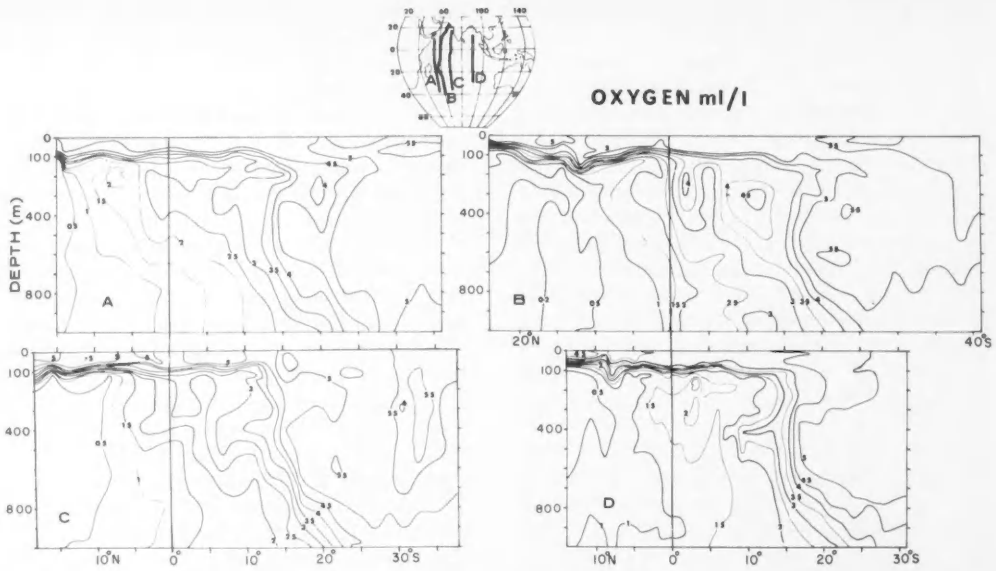

FIGURE 3.—Vertical distribution of oxygen along four north-south transects in the Indian Ocean: A - lat. 14°N to 36°S at long. 55°E (February-March); B - lat. 24°N to 41°S at long. 60°E (August-November); C - lat. 18°N to 37°S at long. 70°E (May-July); D - lat. 13°N to 30°S at long. 92°E (August-September). (Charts reproduced from Wyrtki, 1971.)

flows along the zone where the thermocline slopes upward toward the Equator between lat. 10°S and 20°S. The general distribution of subsurface isotherms is more or less similar across the full breadth of the equatorial region.

Wyrtki's figure (1971:38) indicates the presence of cold surface water in the northern part of the Bay of Bengal during the NE monsoon. Banse (1960) pointed out that the cold surface water in this region may not be attributed to upwelling, but to a high rate of evaporation caused by the dry air from the continent. The coasts of northwest Australia and Java are other regions reported to have seasonal upwelling. Wyrtki (1961) pointed out that there was intense upwelling in these two areas during the SW monsoon.

It is postulated that in the Indian Ocean wind-driven equatorial upwelling is less intense than in the Atlantic and Pacific oceans and may be totally absent (Taft, 1971). The absence of substantial peaks in the zooplankton biomass along the equatorial regions of the Indian Ocean is consistent with the idea of there being little equatorial upwelling, compared at least with the Pacific (King and Demond, 1953; Reid, 1962; Heinrich, 1968) and the Atlantic (Hentschel, 1933).

In the Indian Ocean seasonal changes in surface salinity are more pronounced in the Arabian Sea and the Bay of Bengal than in any other region (see Wyrtki, 1971). Throughout the year the surface salinity was greater in the Arabian Sea than in the Bay of Bengal. During the NE monsoon surface salinity becomes very low (30-33‰ in the Bay of Bengal; advection of low-salinity water occurs from the Bay of Bengal toward the western Indian Ocean. As the Monsoon Current develops during the SW monsoon, a tongue of high-salinity water flows eastward.

RESULTS

Geographical Distribution of *Nematoscelis gracilis*

Indian Ocean

Two forms considered to be ecophenotypes of *N. gracilis* are recognized to occur in the Indian Ocean: an "old form" which is identical in morphological character to the typical form described by Hansen (1910) from waters of the Indo-Australian Archipelago, and a "new form" which

is distinguished from the typical form on the basis of the difference in dimension of the proximal process of the petasma. In the old form the proximal process does not reach the distal end of the median lobe, whereas in the new form it is extremely long, reaching far beyond the distal end of the median lobe. The proximal process of the old form is serrated at the distal end and that of the new form is without any serration. There is also an apparent size difference between the two forms; the body length of the old form is found to be significantly larger than that of the new form. Moreover, the upper lobe of the eye of the new form is narrower than that of the old form. Along the equatorial zone, where the distributions of the two forms overlap, another form, which is recognized to be "intermediate" of the old and new forms with regard to the length of the proximal process, is also encountered. All three forms are distinguishable only in mature adults: males on the basis of structural differences of the petasma and females on the basis of differences in the body lengths and eye shape. Further discussion of them will appear in a forthcoming taxonomic paper (manuscript).

Nematoscelis gracilis is by far the most abundant species of *Nematoscelis* in the tropical regions of the Indian Ocean, including the Arabian Sea and the Bay of Bengal (Figures 4, 5). Along the full extent of the ocean at the Equator this species was found to be distributed between lat. 20°N and 20°S. The southern limit extended farther south along the regions of the western and eastern boundary currents, the Mozambique Current, and the West Australian Current, respectively. Larvae and juveniles were caught year-round from all geographical areas within the distributional range of the species. Therefore, spawning apparently occurred everywhere within that range. Larvae consisted of metanauplii, calyptopes, and furcilias; metanauplii were undoubtedly underestimated since they (body length < 1 mm) could have been washed away through mesh apertures of the net.

During the NE monsoon maximum numbers of larvae and juveniles per sample were caught off the coast of southeast India (Figure 4a). For example, during *Kistna* cruise 26, 840 individuals were caught at station 704 (lat. 13°N, long. 81°E); and 764 individuals from station 705. Four stations had numbers exceeding 300 per sample from the same area. However, during the SW monsoon maximum abundance was in the western Indian Ocean north of the Equator (Figure 4b). Both larvae and juveniles were absent from the northern and northeastern Arabian Sea. There the oxygen concentration in the subsurface waters is as low as 0.1 ml/l (see Figure 2B). They were also absent to the north of lat. 10°N along the west coast of India; but during the NE monsoon they were caught as far north as lat. 15°N in the coastal waters of southwest India. The North Equatorial Current, flowing westward, has a northwestward component after passing the southern tip of India during the early part of the NE monsoon, bringing a spawning population of this species as far north as lat. 15°N. In the area of the Mozambique Current, larvae and juveniles were caught only as far south as lat. 30°S.

Adults of the old form are confined mostly to the Arabian Sea and the Bay of Bengal and the new form to areas of the Southwest Monsoon Current and the South Equatorial Current which is situated south of the Equator. During the NE monsoon old forms are frequently caught in the areas of the North Equatorial Current, whereas new forms occur only in the Equatorial Countercurrent and south of it. The two forms overlap in distribution along the northern boundary of the Countercurrent from east of long. 75°E. In the eastern Indian Ocean the distribution of old forms extends farther south (as far as lat. 14°S) (Figure 5a). "Intermediate forms" were encountered all along the overlapping zone. They were present along the western and eastern boundaries of the ocean. Most transport of the intermediate forms to the west is through the North Equatorial Current. In the South Equatorial Current it was found only at one station (*Koyo Maru* cruise 14, station 19: lat. 13°49′S, long. 94°16′E). In the western Indian Ocean there was no overlap in distribution of the forms, and the new forms did not occur north of the Equator. Moreover, during this period the Somali Current flows southwestward so that it brings the old form as far south as lat. 3°S. Therefore, the pattern of distribution of the two forms in the upper layer may be influenced by the direction of water flow in the equatorial current system which is subject to seasonal changes. During the NE monsoon no samples were taken from the Mozambique Current area north of lat. 30°S. However, mature adults of the new form were caught in one sample taken from the southeast coast of Africa (*Natal* cruise 6, day station 161: lat. 34°21′S, long. 26°21′E). Thus it appears likely that the Mozambique Current, which is stronger during the NE monsoon than in the opposite season (as judged

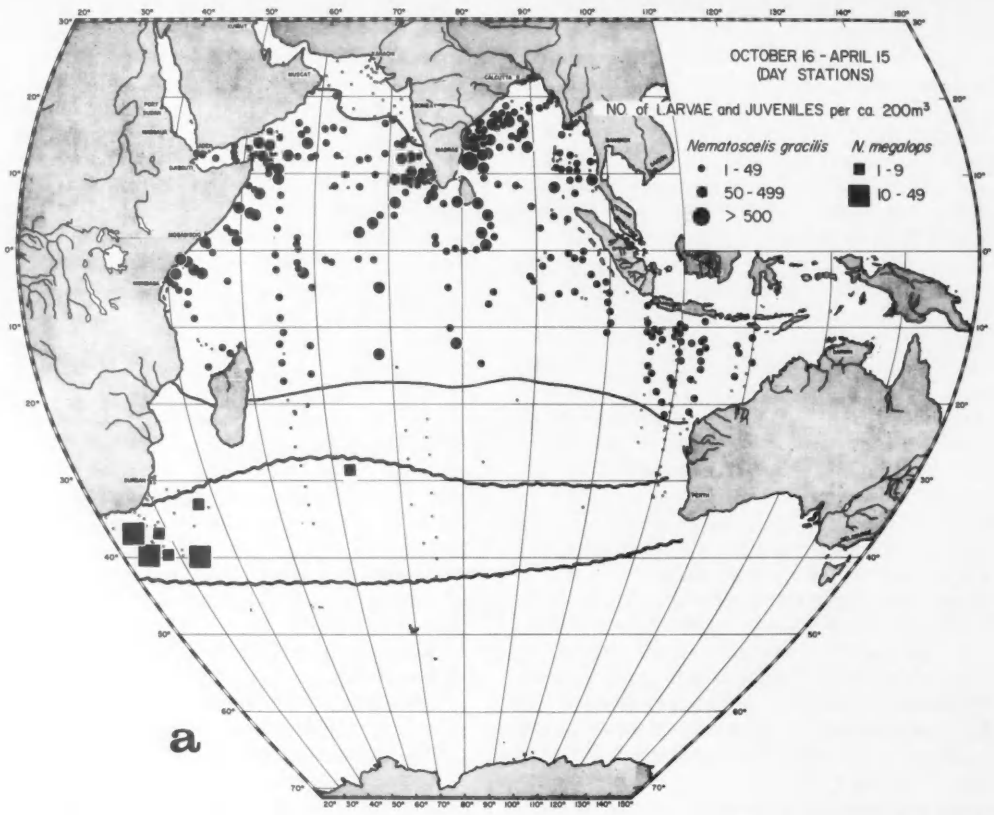

FIGURE 4.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis gracilis* and *N. megalops* in the Indian Ocean: a - NE Monsoon period. (Solid lines represent approximate distribution boundaries of *N. gracilis* and wavy lines represent those of *N. megalops*.)

from Figures 14.1 and 14.2 of Neumann and Pierson, 1966) and to which the South Equatorial Current contributes, transports some of the new forms to the south and the Agulhas Current transports them to the tip of South Africa.

During the SW monsoon the distribution of the new form is much broader in the west than in the east (Figure 5b). As the strong Somali Current begins to flow northeastward, a great deal of Southern Hemisphere water is brought to the north along the African coast. Thus the population of the new form is brought north of the Equator. It was caught as far north as lat. 8°N along the coast of Somalia; but it did not reach the upwelling areas of the Arabian coast. It has been suggested that the Somali Current turns eastward after reaching lat. 8°N and joins the Southwest Monsoon Current flowing east (Taft, 1971); the distribution of the new form in the upper layer follows the same pattern (Figure 5b). Except in the area of the Somali Current, the overlapping zone was confined to the eastern ocean. The intermediate forms were distributed across the equatorial ocean. In the region of the Mozambique Current new forms were found as far south as lat. 30°S.

Populations of the old form in the Bay of Bengal and the Arabian Sea show seasonal changes in the abundance of larvae and juveniles (Figure 6). All the available IIOE plankton samples from these two areas were used to prepare these monthly frequency distributions. In the Bay of Bengal the highest frequency of calyptopis larvae was observed in February, whereas in the Arabian Sea it

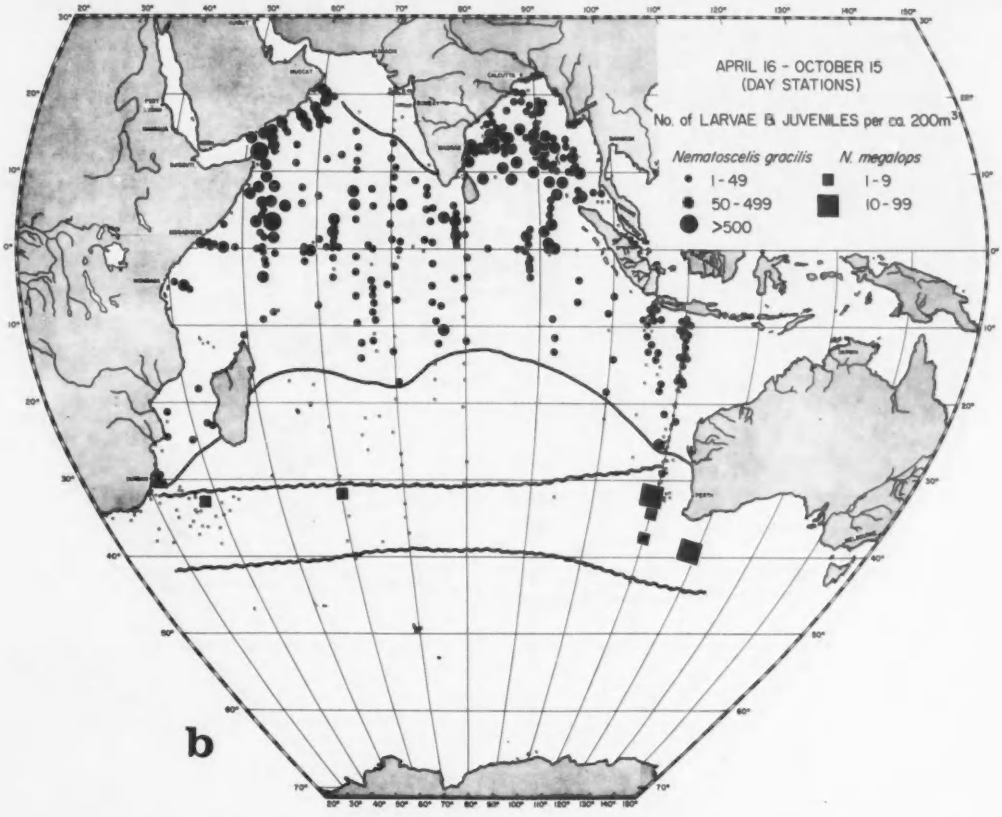

FIGURE 4.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis gracilis* and *N. megalops* in the Indian Ocean: b - SW Monsoon period. (Solid lines represent approximate distribution boundaries of *N. gracilis* and wavy lines represent those of *N. megalops*.)

was during August and December. (In both areas metanauplii were clearly underestimated.) A Student's t-test carried out on means of developmental stages during February, August, and December indicated that the frequencies of larvae in the Bay of Bengal were significantly different ($P < 0.01$) from those in the Arabian Sea during the same months. Frequencies during other months were not significantly different between the two populations. Since most of the developmental stages were caught each month, it appears that spawning is continuous; only the rate of production is subjected to seasonal changes.

The distributional patterns of the two forms of *N. gracilis* so far discussed are based on adults caught from the upper 200-m layer. As pointed out before, the vertical distribution of this species extends much greater than this depth. Figure 7a shows the distributions of new and old forms based on deeper samples. Evidently these are similar to those based only on the upper layer samples (cf. Figures 5, 7a). Both forms were caught from the same station only near the Equator, and intermediate forms were found only at the areas of overlap near the Equator.

Atlantic Ocean

Nematoscelis gracilis has not been reported from the tropical Atlantic Ocean, nor was it found in any collections examined during the present survey. The only record from the Atlantic Ocean was from the southwest coast of Africa (Lusiad VII-IKMT, station 63-539, lat. 33°47'S, long.

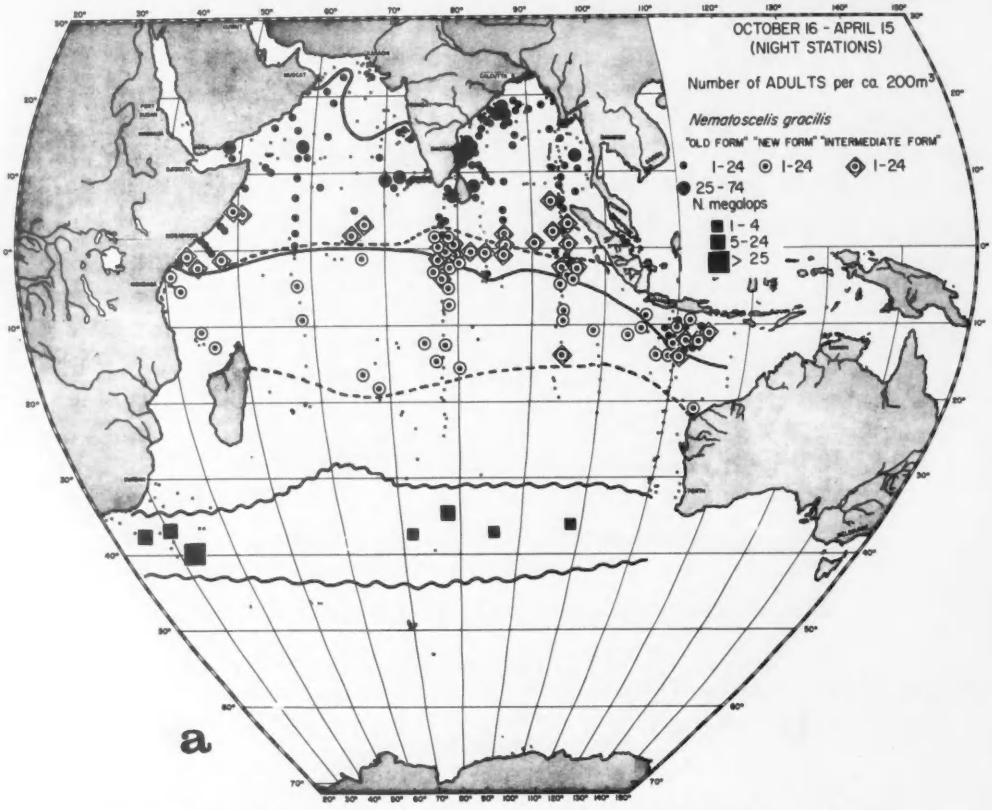

FIGURE 5.—Locality records and nighttime abundance of *Nematoscelis gracilis* and *N. megalops* adults in the Indian Ocean: a - NE Monsoon period. (Solid lines represent approximate boundaries of distribution of *N. gracilis* "old form," broken lines represent those of "new form," and wavy lines those of *N. megalops*.)

15°47′E, 5 June 1963). (See Figure 14b.) Three adult males and one female belonging to the new form were caught at this station, but no old form was found. Probably these new forms were transported westward by the Agulhas Current (Figure 7a).

Pacific Ocean

Nematoscelis gracilis is recorded from the equatorial zone of the Pacific (Brinton, 1962). Populations of this species were also shown to have been carried by the Kuroshio system to as far as lat. 40°N, east of Japan. The numerical density was found to be much higher in the east than in the west. In the present survey based on mid-water trawls from the Pacific, a similar pattern of distribution was observed (Figure 7a). The new forms were also found to occur in the Pacific, but only south of the Equator. There Reid (1965) recognized an eastward flow at about 400-800 m (on the basis of acceleration potentials at 125 cl/ton (lat. 2°-8°S) and 80 cl/ton (lat. 8° - 20°S) δ T). However, in the eastern Pacific the same latitudes are occupied by old forms where Reid (1965) and Love (1972) reported a narrow tongue of low oxygen, as low as 0.2-0.5 ml/l, extending westward. The contour of oxygen concentration of 0.5 ml/l extended as far west as long. 130°W between the Equator and lat. 10°S (at 160 cl/ton δ T surface, 150-200 m). This may account for the fact that new forms do not reach eastward to the coasts of Chile and Peru. The association of old forms with oxygen-poor

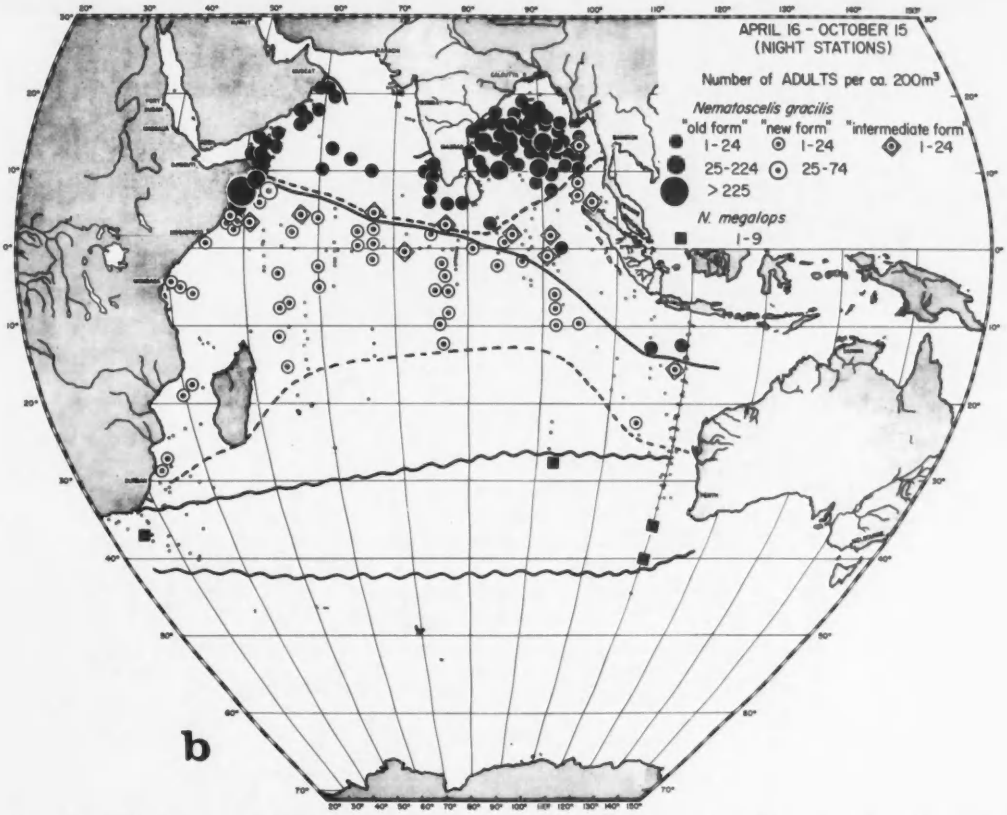

FIGURE 5.—Locality records and nighttime abundance of *Nematoscelis gracilis* and *N. megalops* adults in the Indian Ocean: b - SW Monsoon period. (Solid lines represent approximate boundaries of distribution of *N. gracilis* "old form," broken lines represent those of "new form," and wavy lines those of *N. megalops*.)

water is evident from these comparisons. *Nematoscelis gracilis* old form is the dominant *Nematoscelis* species occurring in the eastern tropical Pacific. Along the coasts of Peru and Chile this form is now known to be distributed as far south as lat. 33°S (personal observation in a sample collected by Antezana). Only old forms were found in the China Sea and in oceanic waters of the Kuroshio system. However, the new and old forms cooccurred in the Timor, Banda, Celebes, Halmahera, and Molucca seas. The Indian Ocean populations of both forms are therefore in continuity with those of the Pacific. In the Pacific the eastern and western populations of the species as a whole are linked along the equatorial zone between lat. 0° and 10°N (Brinton, 1962). Brinton has pointed out that the lat. 20°N-20°S range of *N. gracilis* in the east and the lat. 10°N-10°S range in the west corresponds reasonably well to the range of the equatorial water mass (Sverdrup, Johnson, and Fleming, 1942).

Geographical Distribution of *N. megalops*

Indian Ocean

Nematoscelis megalops was recorded during the IIOE between lat. 30°S and 45°S. This is the area of transition between subantarctic and Indian Central water (Sverdrup et al., 1942). The number of samples collected from this zone is too scanty to permit a seasonal study. Larvae, juveniles, and adults were caught during both seasons along the

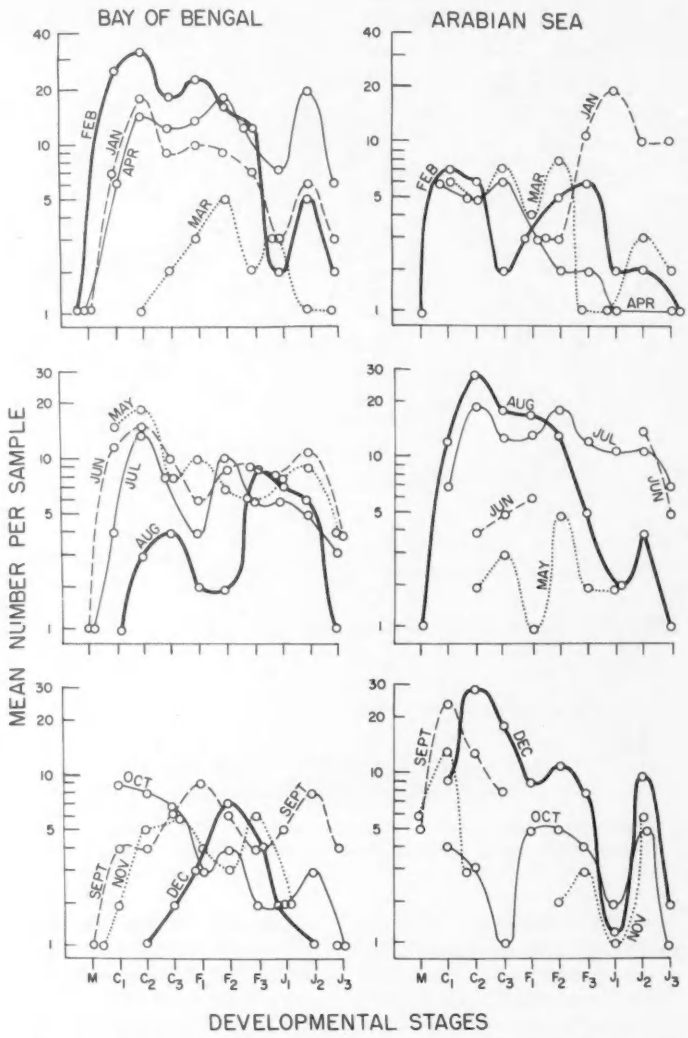

FIGURE 6.—Frequency distribution of developmental stages of *Nematoscelis gracilis* "old form" in the Bay of Bengal and the Arabian Sea. (Number of samples used to calculate monthly averages ranged from 11 to 18.)

full extent of the transition zone (Figures 4, 5). In the western Indian Ocean, the maximum number of larvae (as many as 280 larvae per sample) was caught during October 1962 (*Natal* cruise 5). In the east, *Diamantina* cruise 3/62 caught up to 90 larvae per sample during September 1962. Although Boden (1954) reported this species in the region of the Mozambique Current, I did not find it in meter-net samples or mid-water trawls taken north of lat. 34°S in waters of southeast Africa (Figure 7b). (Trawls were made during the October-November period.) However, the northern boundary of distribution appears to lie between lat. 28°S and 30°S. The northernmost record of this species was at lat. 28°18′S, long. 62°33′E (*Vitiaz* 36, station 5323).

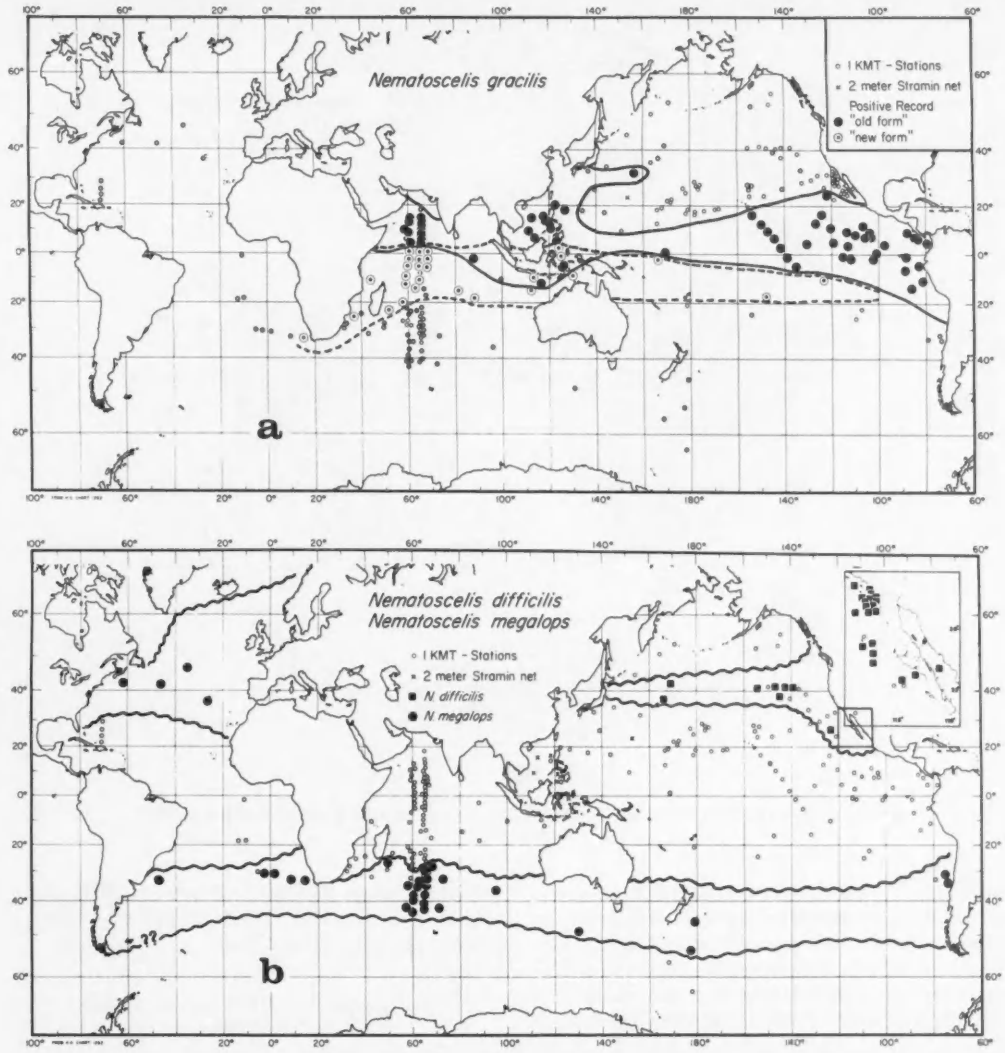

FIGURE 7.—Worldwide distribution of *Nematoscelis* based on mid-water trawls: a - *N. gracilis* "old" and "new" forms; b - *N. difficilis* and *N. megalops*. (Solid lines represent approximate boundaries of distribution of old form, broken lines represent those of new form, and wavy lines represent distributional boundaries of *N. difficilis* and *N. megalops*. Boundaries are based on literature records and present evidence.)

Atlantic Ocean

Nematoscelis megalops appears to have a wider north-south range in the Atlantic than in other oceans. The southernmost record in the North Atlantic was in the region of the Canary Current (Figure 8a). Larvae and juveniles were frequently caught between lat. 40°N and 53°N. Literature records of this species in the North Atlantic are as far north as lat. 68°N (Zelikman, 1964). Moore (1952) recorded this species from lat. 35°N to 55°N. It occurs in the Mediterranean Sea (Ruud, 1936). In the South Atlantic it was collected by the Lusiad Expedition between lat. 25°S and 30°S

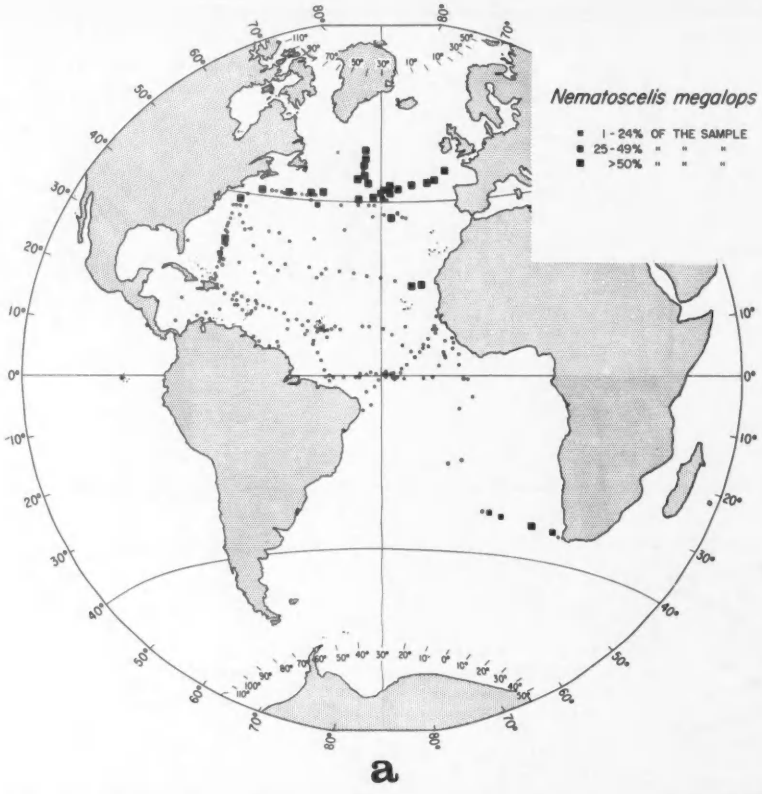

FIGURE 8.—Distribution of *Nematoscelis* in the Atlantic Ocean based on plankton samples: a - *N. megalops*.

(Figure 8a). Boden (1954) recorded this species from the Benguela Current as far north as lat. 22°S. From the western part of the South Atlantic no data is available. The only literature record is from the Brazil Current area, between lat. 45°S and 50°S and long. 62°W and 68°W (Ramirez, 1971).

Pacific Ocean

Nematoscelis megalops and *N. difficilis* are a recognized sibling species pair, occupying transoceanic belts of the transition zones of the South and North Pacific oceans respectively (Brinton, 1962). During the Downwind Expedition, Brinton found *N. megalops* distributed between lat. 33°S and 48°S in midocean. The Monsoon Expedition caught it as far south as lat. 54°21′S (Figure 7b). Along the coasts of Chile between lat. 30°S and 50°S this species was caught by MV-65 (*Anton Bruun*), Piquero III, and Scorpio I expeditions.

Geographical Distribution of *N. difficilis*

Nematoscelis difficilis is endemic to the North Pacific, occupying the North Pacific Drift and the California Current (Figure 7b). It was reported during Transpacific Expedition from seven stations located east of Japan (Brinton, 1962). In the present study it was found in mid-water trawls from near lat. 40°N between long. 130°W and 160°W. Along the North American coast, the distribution extends northward to lat. 51°N (Banner, 1949) and southward to lat. 20°N (Brinton, 1962). It is common in the cold water of the California

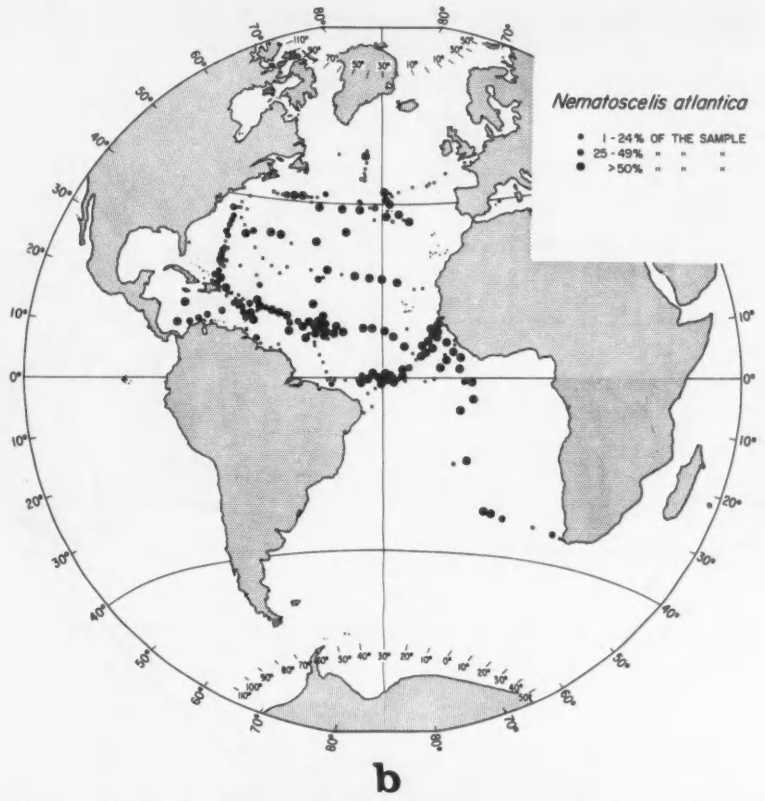

FIGURE 8.—Distribution of *Nematoscelis* in the Atlantic Ocean based on plankton samples: b - *N. atlantica*.

Current and caught frequently in mid-water trawls in the San Diego Trough area. This species was also caught in the Gulf of California by the Vermilion Sea Expedition; however, this population is believed to be separated, perhaps seasonally, from that on the west side of Baja California due to the influx of warm water from the south at the mouth of the Gulf (Brinton, 1962). Literature records and present evidence indicate that the ranges of *N. megalops* and *N. difficilis* do not overlap.

Geographical Distribution of *N. atlantica*

Indian Ocean

This species has not been reported previously from the Indian Ocean. In the IIOE collections there were frequent occurrences of this species, but only in the midlatitudes (lat. 15°-40°S) of the Southern Hemisphere (Figure 9a, b). *Nematoscelis atlantica* lives in the region of the Indian Ocean central water mass. Larvae and juveniles were caught from most stations occupied within the range of distribution of the species. Moreover, there were no obvious differences between seasonal distributions. IIOE samples included many adults from west of Australia and the Agulhas Current (Figure 10a, b). In the mid-water trawls it was caught between lat. 11°S and 42°S along long. 60°E (Figure 11a).

Atlantic Ocean

Nematoscelis atlantica was observed in many samples from the North Atlantic (Figure 8b). Un-

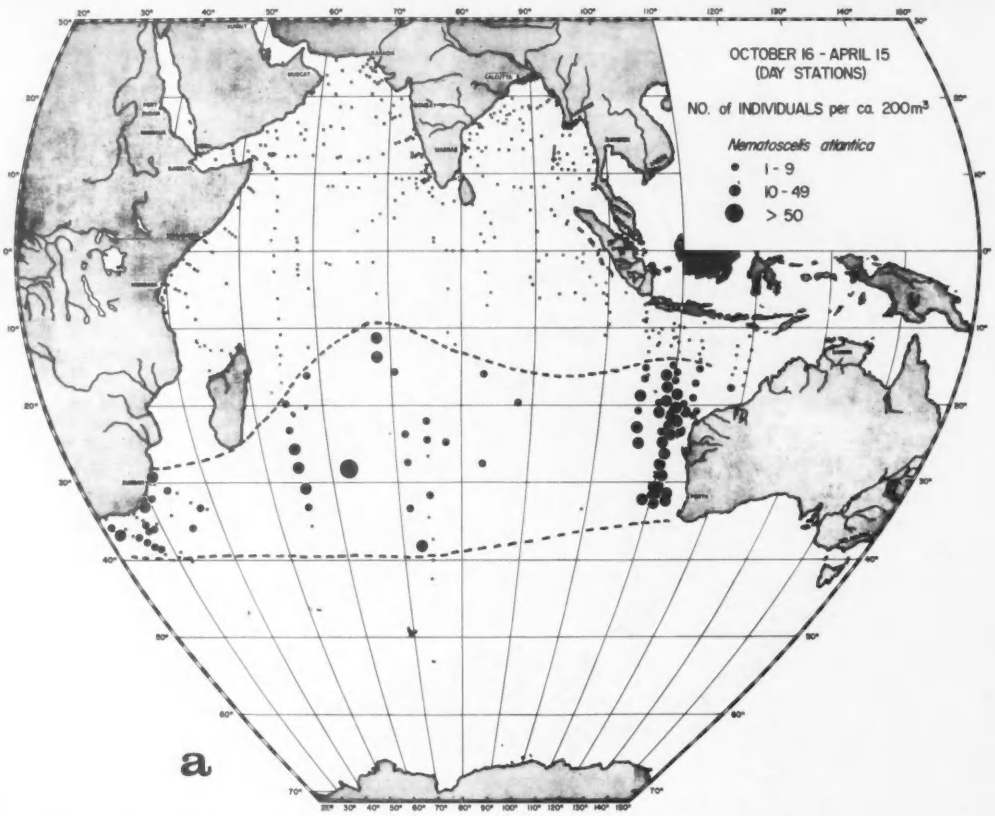

FIGURE 9.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis atlantica* in the Indian Ocean: a - NE Monsoon period.

like in the Pacific and Indian oceans, this species also occupies the Atlantic equatorial zone providing communication between North and South Atlantic populations. The German South Polar Expedition (Zimmer, 1914) first recorded the north-south continuity of *N. atlantica* in the Atlantic. In the eastern Atlantic between the Equator and lat. 40°N, *N. atlantica* constituted over 50% of the total *Nematoscelis* present in each sample. The northernmost record was at lat. 52°N (*Atlantis II*-9, station 371). This species was not reported previously from the North Atlantic central gyre (Mauchline and Fisher, 1969). In the present collection many larvae, juveniles, and mature adults were recorded from this area. Mediterranean Sea records come from Ruud (1936) and Casanova-Soulier (1968). In the South Atlantic it was present in the Lusiad collections (Figure 11a). Literature records in the South Atlantic show that it occurs in the Benguela Current, extending as far as lat. 40°S (Mauchline and Fisher, 1969). No samples were available from the areas of the Argentine Basin.

Pacific Ocean

In the Pacific, *N. atlantica* lives in the central water masses of both hemispheres (Figure 11a). The approximate boundaries of distribution are between lat. 13° and 38° in each hemisphere (Brinton, 1962). It was not caught in the Naga collections from the Indo-Australian Archipelago. The North Pacific population of this species appears to be separated from those of the South Pacific and Indian Ocean regions. It may be possible that communication exists between Indian and South Pacific populations through the oceanic waters south of Australia.

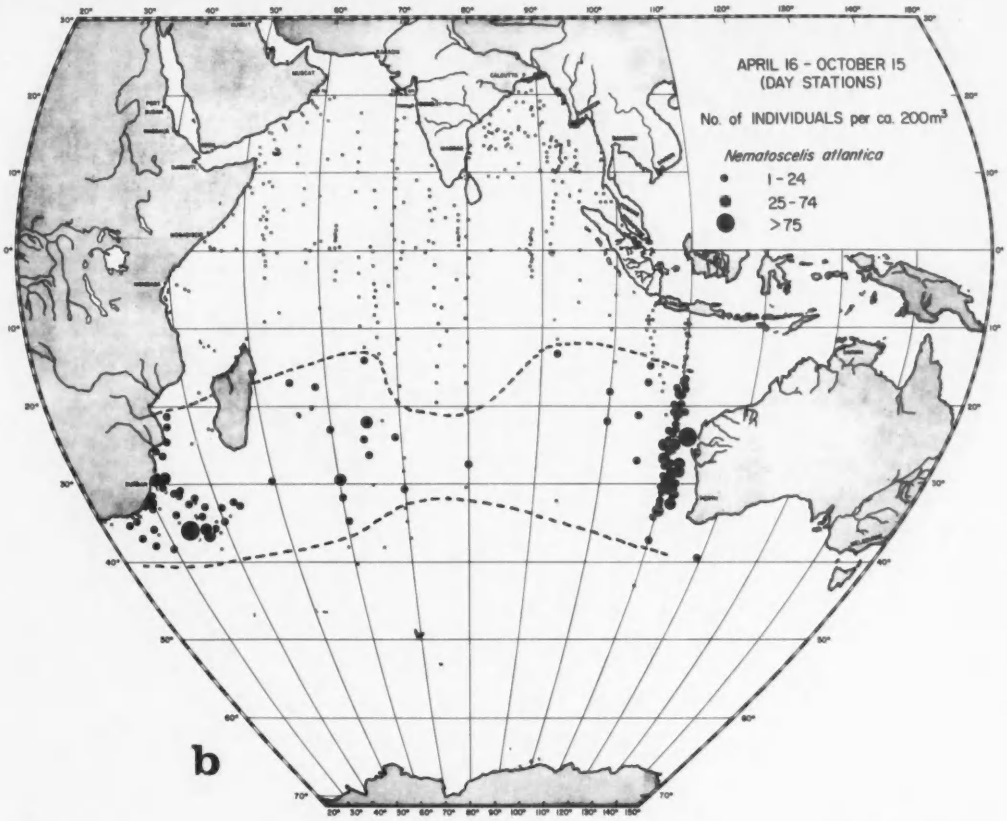

FIGURE 9.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis atlantica* in the Indian Ocean: b - SW Monsoon period.

Geographical Distribution of *N. microps*

Indian Ocean

Nematoscelis microps has wider ranges of distribution than *N. gracilis* and *N. atlantica*. This species penetrates the Arabian Sea and the Bay of Bengal only at their western and eastern sides respectively (Figure 12a, b). The northernmost record of this species in the western Arabian Sea was at lat. 14°N and that in the eastern side of the Bay of Bengal at lat. 19°N off the coast of Burma. It does not live in the poorly oxygenated subsurface waters of the Arabian Sea and Bay of Bengal. In midocean the northern boundary does not extend north of lat. 6°N and the southern boundary not beyond lat. 30°S. It was caught less frequently from the southern central gyre south of lat. 10°S. *Nematoscelis microps* is a predominant species of the South Equatorial Current and the West Australian area. The Agulhas Current apparently brings it around the tip of South Africa.

There was not much seasonal change in the distribution of this species in the Indian Ocean. Larvae and juveniles were present in the Somali Current area during both monsoon seasons but were carried as far north as lat. 14°N only during the SW monsoon. They were present throughout the year in the Andaman Sea area. During the NE monsoon adults were not caught in the Somali Current area north of the Equator, whereas they were present as far north as lat. 12°N during the opposite season when the flow is northeastward (Figure 13a, b). Adults occurred in the North Equatorial Current area during the NE monsoon

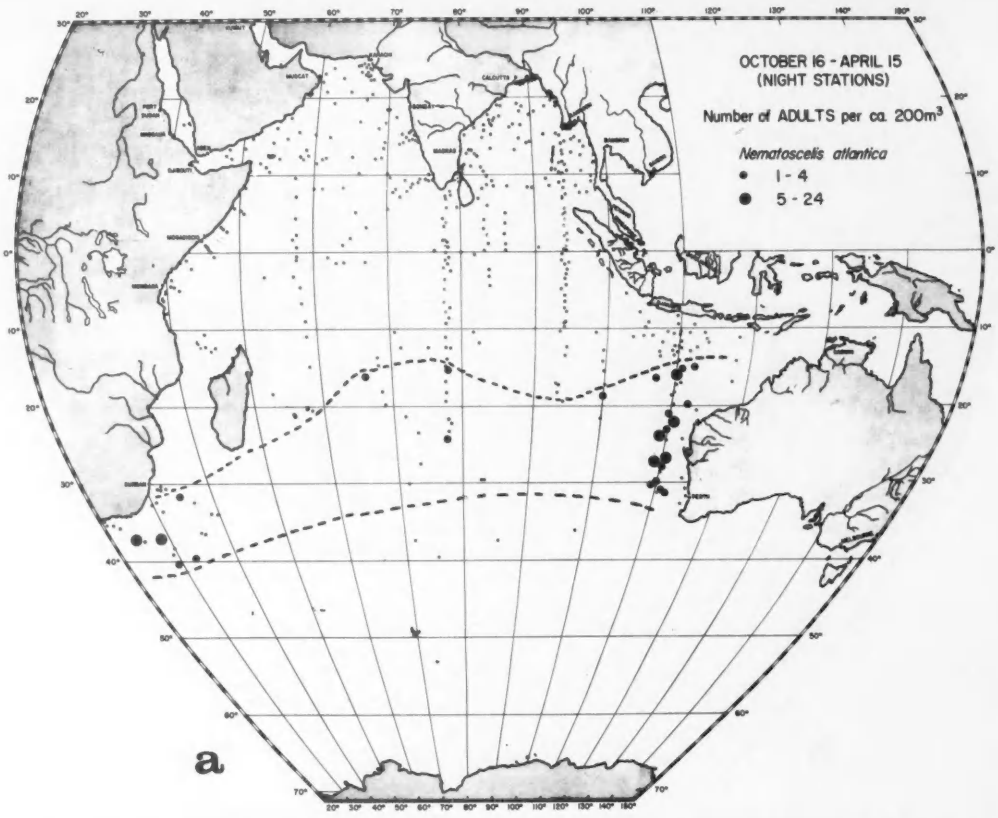

FIGURE 10.—Locality records and nighttime abundance of *Nematoscelis atlantica* adults in the Indian Ocean: a - NE Monsoon period.

but were not caught there during the opposite season when the Monsoon Current replaces the North Equatorial Current. During the SW monsoon none of the stations north of the Equator between long. 50°E and 90°E contained adult specimens (Figure 13b). Evidently this species does not reach the coast of India. In the mid-water trawls *N. microps* was caught between lat. 10°N and 41°S (Figure 11b), but north of lat. 2°N this species was caught from only one station (*Anton Bruun* cruise 3, station 146, lat. 10°09′N, long. 59°55′E).

Atlantic Ocean

From the Atlantic Ocean there are literature records of scattered occurrences of this species between lat. 40°N and 40°S. Moore (1952) reported that this species occurred in the western Atlantic north of the equator to lat. 40°-45°N, in the region of the Gulf Stream. The most northerly record in the eastern ocean was from lat. 59°39′N (Illig, 1930), although most other records lie south of lat. 40°N. In the present survey it was caught between the Equator and lat. 40°N and was relatively more abundant in the western ocean than in the east (Figure 14a). It was not present in many samples taken from the North Atlantic central gyre. There were a few doubtful records of this species from the Mediterranean Sea (Ruud, 1936; Bacescu and Mayer, 1961). In the South Atlantic it was caught by Lusiad and *Atlantis II* - 31 expeditions (Figure 11b).

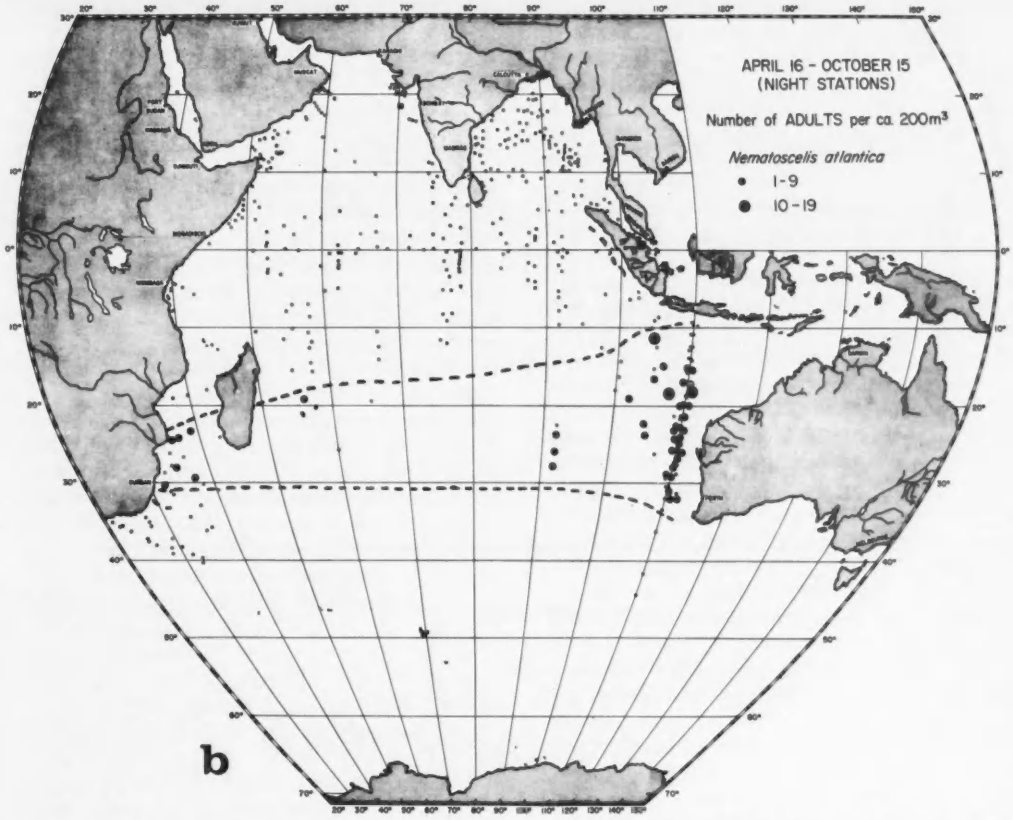

FIGURE 10.—Locality records and nighttime abundance of *Nematoscelis atlantica* adults in the Indian Ocean: b - SW Monsoon period.

Pacific Ocean

North and South Pacific populations of *N. microps* are in communication with each other across the western equatorial Pacific (Figure 11b). This species is absent along the eastern boundary currents (California Current and Peru Current) and also from the poorly oxygenated subsurface waters of the eastern tropical Pacific. *Nematoscelis microps* was also caught less frequently in the eastern North Pacific central water mass than in the western North Pacific central water mass. In the equatorial region this species is known to occur only west of long. 110°W (Brinton, 1962). It is also recorded from the China Sea and the regions of the Timor, Molucca, and Banda seas. The populations of the Indian and Pacific oceans are probably in communication with each other through the straits of Timor, Banda, Molucca, and Halmahera.

Geographical Distribution of *N. lobata*

Hansen (1916) described *N. lobata* from the Philippines. He found it at only two localities: lat. 13°43′N, long. 121°E and lat. 7°07′N, long. 125°40′E. *Nematoscelis lobata* appears to be endemic to the semi-isolated seas around the western side of the Philippines. In the present survey it was caught mostly from the Sulu Sea area (Naga Expedition) (Figure 15). At station S11B-205, five mature males and six females were caught in a 2-m-net collection, 0-500 m (lat. 6°35′N, long.

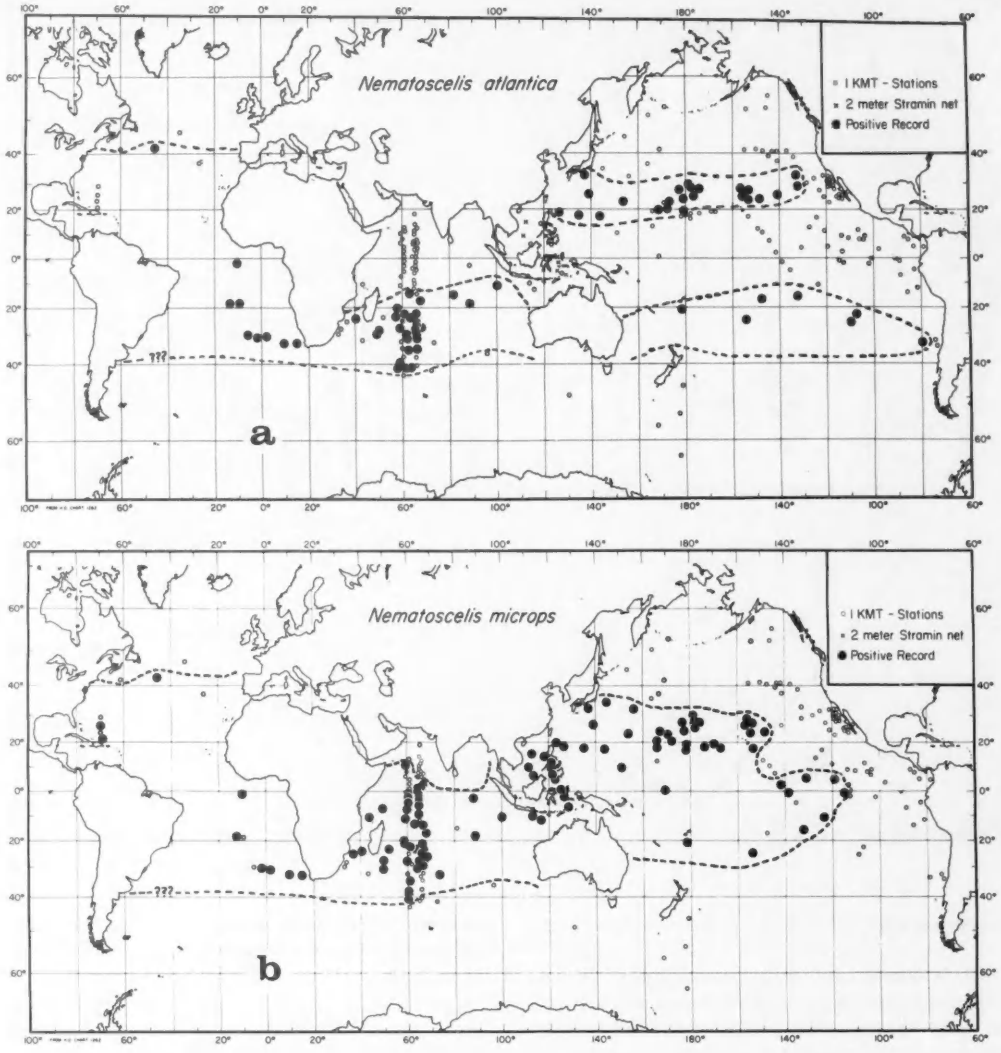

FIGURE 11.—Worldwide distribution of *Nematoscelis* based on mid-water trawls: a - *N. atlantica*; b - *N. microps*. (Broken lines represent approximate boundaries of distribution of the species based on literature records and present evidence.)

122°27'E; 29 April 1961). At six other stations only mature females were caught. The petasma, particularly the broad median lobe with its convex inner and outer margins, is an excellent diagnostic feature of this species. The shape of the keel on the carapace of both sexes is also different from other *Nematoscelis* species. *Nematoscelis lobata* is not reported from any other place, including the Siboga collections from the East Indian Archipelago and the Troll Expedition collections made along the eastern coast of the Philippines (Figure 15). This species appears to be absent from the South China Sea and the Gulf of Thailand (Brinton, manuscript).

Geographical Distribution of *N. tenella*

Indian Ocean

The geographical distribution of *N. tenella* is similar to that of *N. microps*. This species lives in the equatorial and central water masses of all oceans. In the Indian Ocean most records came from between lat. 7°N and 38°S except in the eastern and western boundary current areas (Figures 16a, b; 17a, b). It was most frequently caught in the equatorial zone and in the eastern ocean south of the Equator. Larvae and juveniles occurred throughout the range of distribution. There were no seasonal differences in the distribution of larvae and juveniles; however, in the western Indian Ocean north of the Equator they were more abundant during the SW monsoon than in the opposite season. This species penetrates into the Arabian Sea only in the western side. It is absent from the Bay of Bengal. The pattern of distribution of adults was like that of larvae and juveniles (Figure 17a, b). Mid-water trawls caught *N. tenella* between lat. 8°N and 40°S (Figure 18).

Atlantic Ocean

Illig (1930) recorded *N. tenella* from lat. 59°39′N, long. 8°49′W, but all other records are from lat. 35°N to 35°S. Lewis (1954) reported this species off southern Florida. In the present study larvae and juveniles were found to be more abundant in the western North Atlantic than on the eastern side (Figure 14b). Around lat. 40°N, its northern limit, it was caught in five plankton samples. It has not been reported from the Mediterranean Sea. In the South Atlantic this species was found in the Lusiad collections off South Africa. No samples were available from the western South Atlantic nor has it been reported from that region. It is also not known whether this species occurs in the Benguela Current.

Pacific Ocean

Nematoscelis tenella lives in both hemispheres of the Pacific, lat. 35°N-34°S. It does not occupy the more coastal areas of the California Current or its southward extension into the eastern equatorial region (Figure 18). It is also scarce in the region of the Peru Current (Brinton, 1962). In midocean, Brinton recorded it as far south as lat. 34°S. This species appears to be more abundant in the northern central gyre than in the south. It occurs farther east in the tropical belt than *N. microps*. The north-south range is continuous across the Equator. It is a common species in the South and East China seas and also in the Banda, Molucca, and Timor seas. Apparent communication exists between the Indian and Pacific populations.

Faunal Zones and Biogeography of *Nematoscelis*

Faunal regions of the oceanic environment are not as well defined as in the terrestrial habitats. The oceanic environment, as distinguished by Hedgpeth (1957), consists of a system of zonally oriented hydrographic provinces arranged in latitudinal succession within each ocean. In the Atlantic Ocean, Dahl (1894) recognized four epipelagic faunal regions: arctic, subarctic (temperate), subtropical, and tropical. Steuer (1933) described a similar system of classification but included the Pacific and Indian oceans. He recognized circumpolar arctic, circumequatorial tropical, and circumpolar antarctic on a global scale. The arctic region was subdivided into a circumpolar subregion as well as Atlantic and Pacific subarctic subregions. The antarctic region includes the circumpolar antarctic and subantarctic subregions. The tropical region was subdivided into Atlantic and Indo-Pacific provinces. A system of classification based on this and other subsequent works [for example: Deacon (1933, 1937); Radzikhovskaya (1965); Stepanov (1965); Frost (1969); McGowan (1971)] is adapted here and shown in Table 2. The division of the epipelagic environment into faunal zones agrees with the distributional patterns of many planktonic organisms [see McGowan (1971) for examples]. Species of *Nematoscelis* occupy one or more of the subregions (Table 3). As mentioned before, *N. difficilis* is endemic to a zone of transition between subarctic and central water in the North Pacific. Even though this zone (Johnson and Brinton, 1963) does not have as well defined a temperature-salinity envelope as other water masses, it maintains endemic species, as well as the densest part of the overall populations of some subarctic and central species. Evidence is accumulating for the existence of a unique water body in this zone with characteristic hydrographical and faunal properties (McGowan, 1971). The extent and location of an analogous transition zone in the North Atlantic, if such exists, is not

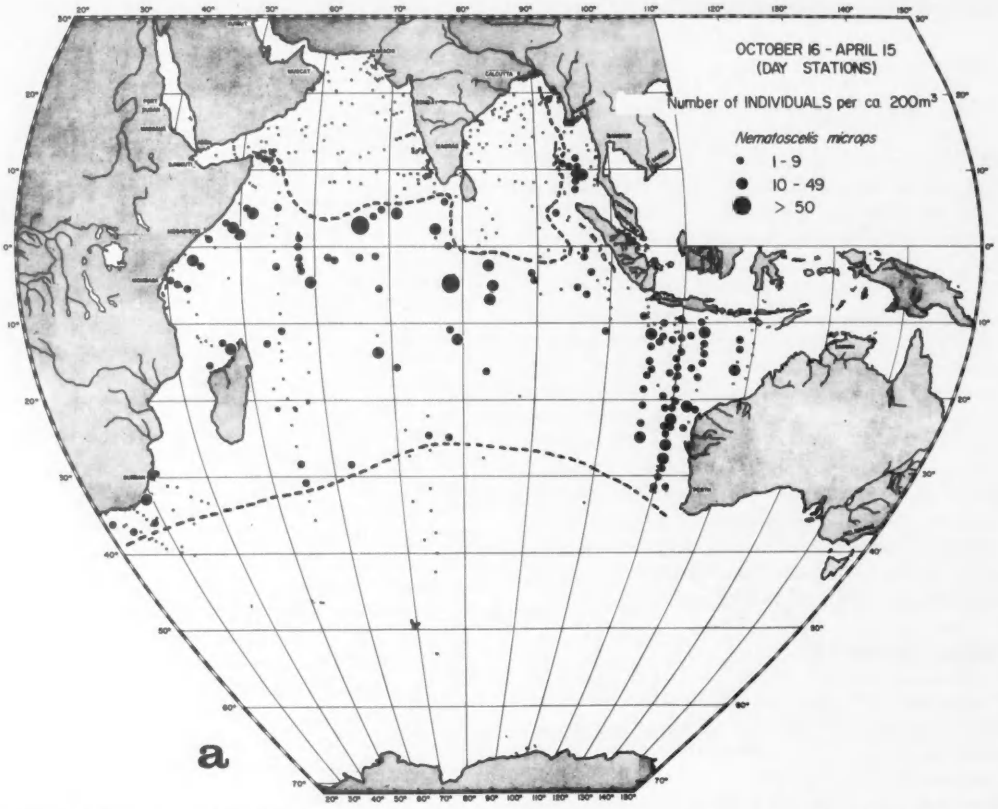

FIGURE 12.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis microps* in the Indian Ocean: a - NE Monsoon period.

TABLE 2.—Biogeographical zones of the oceanic environment.

Zones	Terminology (Regions)	Latitude (approximate)	Subregion
Northern Cold Water	Circumpolar Arctic	>67°N	
	Subarctic (Cold Temperate)	45°-67°N	Subarctic Atlantic Subarctic Pacific
Northern Transitional	———	35°-45°N	Transitional North Atlantic Transitional North Pacific
Warm Water	Northern Subtropical (Warm Temperate)	23°-35°N	Subtropical North Atlantic Subtropical North Pacific
	Tropical	23°S-23°N	Tropical Atlantic Tropical Indo-West Pacific Eastern Tropical Pacific
	Southern Subtropical (Warm Temperate)	23°-35°S	Subtropical South Atlantic Subtropical South Pacific Subtropical South Indian
Southern Transitional	———	35°-45°S	Circumpolar Transitional Region of the Southern Hemisphere
Southern Cold Water	Circumpolar Subantarctic (Cold Temperate)	45°-67°S	
	Circumpolar Antarctic	>67°S	

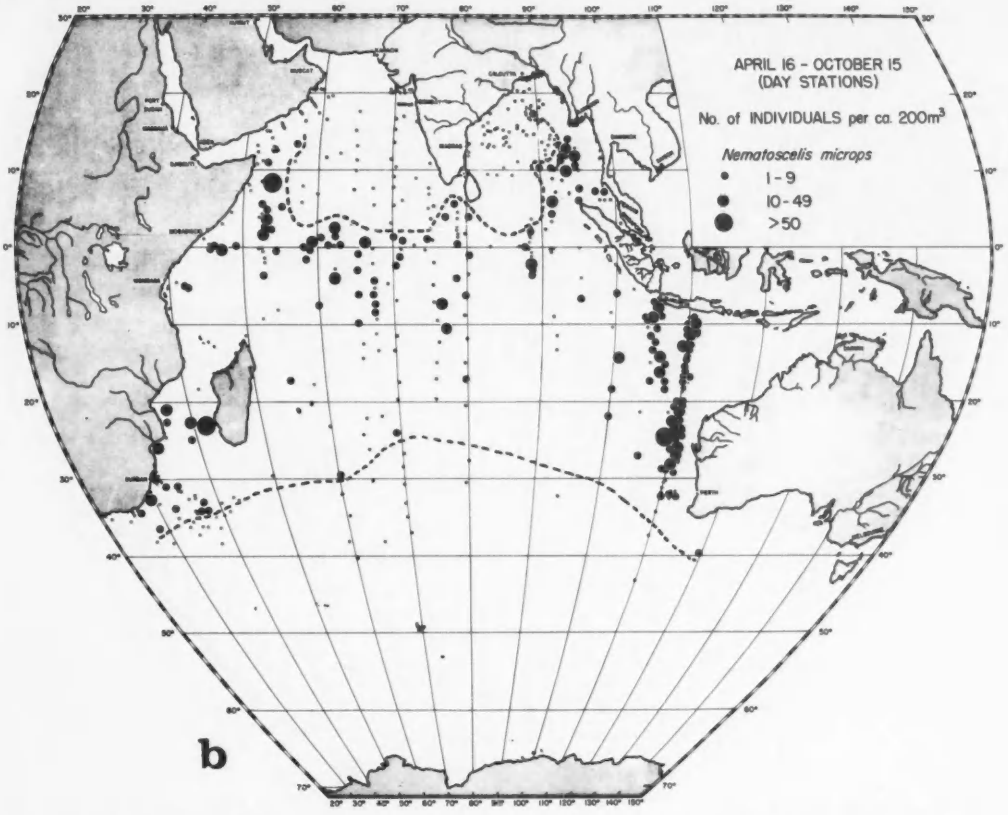

FIGURE 12.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis microps* in the Indian Ocean: b - SW Monsoon period.

TABLE 3.—Biogeographical zones of the oceanic environment and the distribution of *Nematoscelis*. *Both new and old forms. **Old forms only. ***New form expatriate adults only. ****New forms in Mozambique Current area only.

Subregions	*N. difficilis*	*N. megalops*	*N. atlantica*	*N. gracilis*	*N. microps*	*N. tenella*
Subarctic Atlantic		x				
Transitional North Atlantic		x				
Transitional North Pacific	x					
Subtropical North Atlantic		x	x		x	x
Subtropical North Pacific			x		x	x
Tropical Atlantic			x		x	x
Tropical Indo-West Pacific				x*	x	x
Eastern Tropical Pacific				x**		x
Subtropical South Atlantic			x	x***	x	x
Subtropical South Pacific			x		x	x
Subtropical South Indian			x	x****	x	x
Circumpolar Transitional Region of the Southern Hemisphere		x				

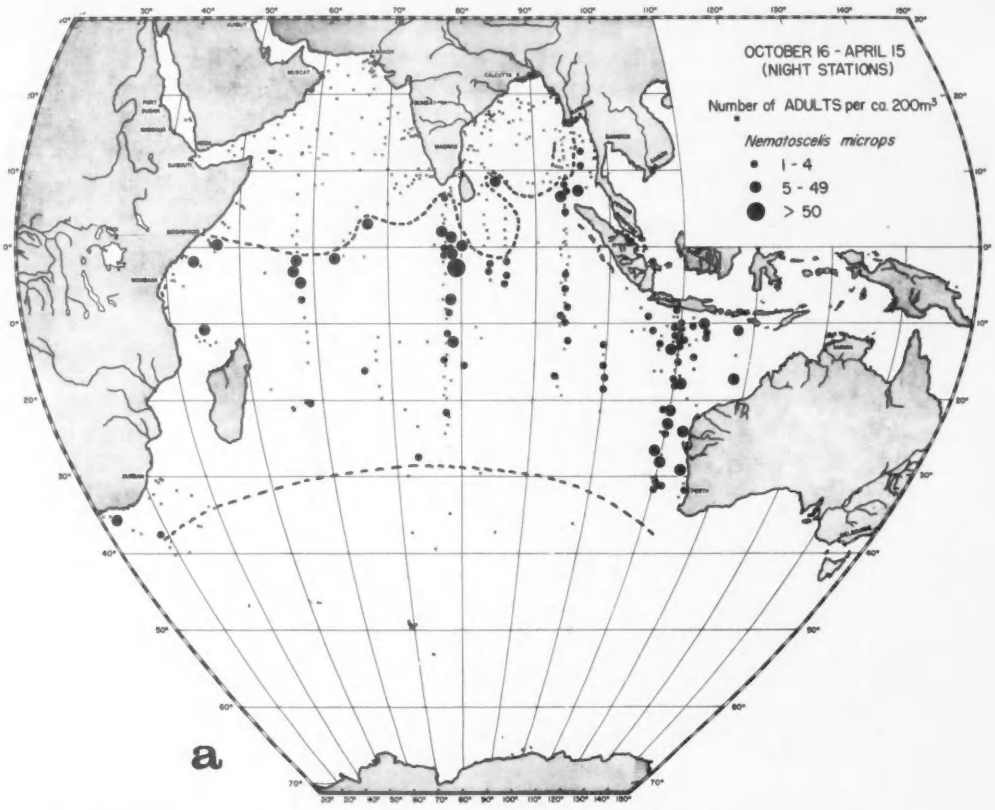

FIGURE 13.—Locality records and nighttime abundance of *Nematoscelis microps* adults in the Indian Ocean: a - NE Monsoon period.

clearly understood. However, lat. 35°-45°N, corresponding to the North Pacific transition, seems to be the extent of the region in the North Atlantic where *N. megalops* (instead of *N. difficilis*) is the most common *Nematoscelis*. *Nematoscelis atlantica*, *N. microps*, and *N. tenella* also appear in the transition zone of the North Atlantic but not in the corresponding zone in the North Pacific. The northeasterly North Atlantic Current carries warmwater species farther north into the transition zone or even beyond to the subarctic subregion. For example, the present survey recorded *N. atlantica* from lat. 52°N (*Atlantis II*-9, station 371). Outside of its main zone in the North Atlantic, *N. megalops* occasionally occurs in the subtropical and subarctic subregions. It is also the most common *Nematoscelis* species of the circumpolar transitional regions of the Southern Hemisphere, while *N. atlantica*, *N. microps*, and *N. tenella* also were occasionally caught there, from the Indian Ocean sector.

The eastern tropical Pacific Ocean is considered a subregion of the warmwater zone because of its characteristic hydrographical and faunal properties. *Nematoscelis gracilis* old form is part of that faunal assemblage. The Indo-West Pacific and eastern tropical Pacific subregions were considered separate from the Atlantic tropical subregion (Ekman, 1953). The distribution of *N. gracilis* and *N. atlantica* presents evidence for this. *Nematoscelis microps* and *N. tenella* are warmwater species, occupying both tropical and subtropical regions (Table 3). Many warmwater planktonic species are restricted to tropical latitudes, whereas others are found only outside of this region (examples in Bieri, 1959; Brinton, 1962; Alvariño, 1965; Baker, 1965; McGowan, 1971). In this respect *N. gracilis* is tropical and *N. atlantica*

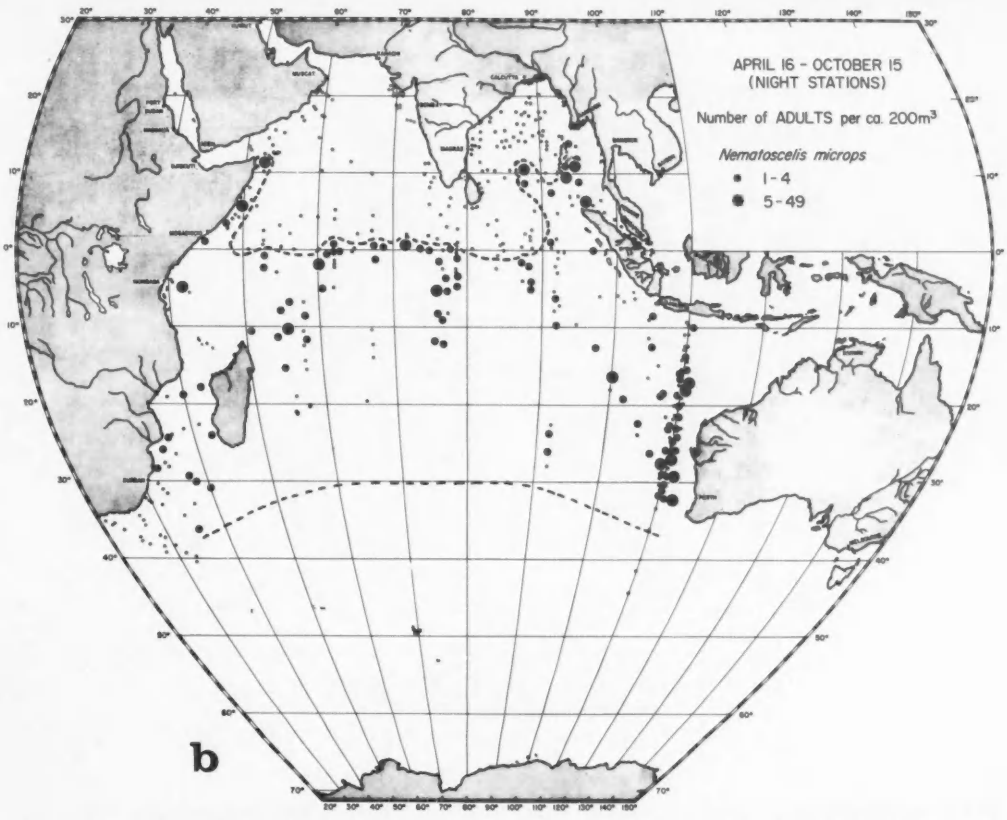

FIGURE 13.—Locality records and nighttime abundance of *Nematoscelis microps* adults in the Indian Ocean: b - SW Monsoon period.

is subtropical. Because the boundaries between the full breadth of tropical and subtropical regions are not well defined hydrographically, it is usually difficult to correlate species' distributional pattern to the hydrographical zones of these two areas.

DISCUSSION

The distributions of *Nematoscelis* species are associated with general hydrographical features in each ocean. In the Indian Ocean the seasonality in abundance of this genus is more pronounced in the Northern Hemisphere than in the south; and it is probably related to changes in monsoonal regimes. The hydrographical features of the Arabian Sea and Bay of Bengal limit the northern boundary of distribution of all species of *Nematoscelis* except *N. gracilis* old form. There appears to be a general break in the north-south midocean distribution of *N. microps* and *N. tenella* near the equatorial zone of the Indian Ocean. Their northern boundary of distribution corresponds to the approximate southern extent of oxygen-poor waters (<1 ml/l) of the Arabian Sea and the Bay of Bengal.

Wyrtki (1973) proposed a division of the Indian Ocean into three circulation systems: a seasonally changing monsoon gyre, a southern subtropical anticyclonic gyre, and the antarctic waters with the Circumpolar Current. One unique feature of the Indian Ocean is the persistence of a hydrochemical front at about lat. 10°S, separating the high-nutrient, low-oxygen content waters of the monsoon gyre from the low-nutrient, high-oxygen content waters of the subtropical gyre. The existence of such a front is very well reflected by the chemical characteristics of the subsurface water

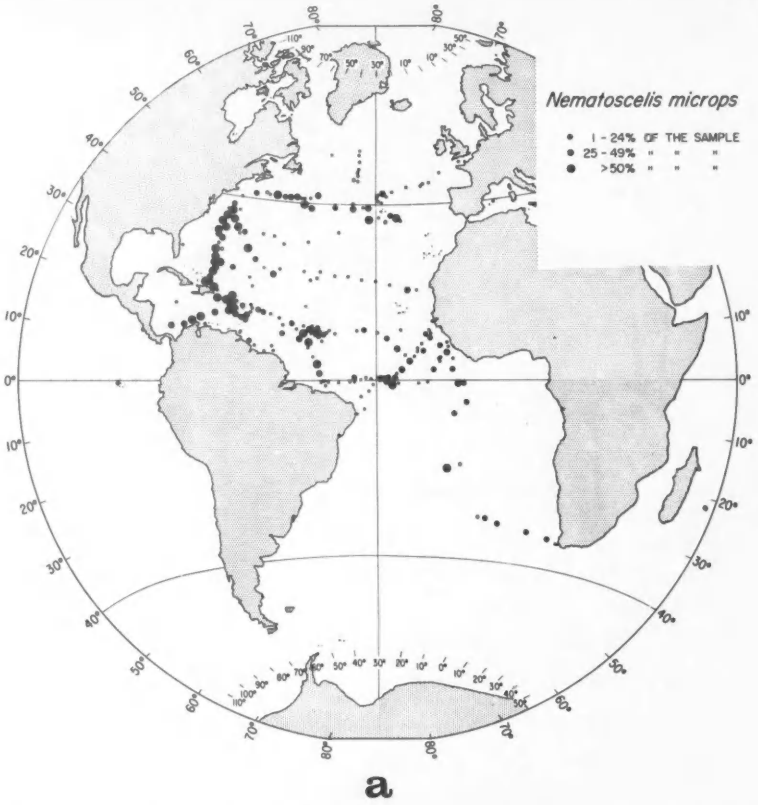

FIGURE 14.—Distribution of *Nematoscelis* in the Atlantic Ocean based on plankton samples: a - *N. microps*.

(Wyrtki, 1973). The boundaries of distribution of many zooplankton species appear to fall within this zonal band. This is also the area of the northern boundary of the subtropical species *N. atlantica*. Evidently the southern boundary of *N. gracilis* new form is not confined to this zone; since the South Equatorial Current carries it as far south as lat. 20°S. The subtropical convergence located at about lat. 40°-41°S separates the southern subtropical anticyclonic gyre and the antarctic circumpolar water. This is the region of the southern boundary of distribution of both the subtropical species *N. atlantica* and the warmwater species *N. microps* and *N. tenella*.

Brinton and Gopalakrishnan (1973) recognized different euphausiid faunal assemblages in the Indian Ocean, each of which is bounded mainly around lat. 10°N, 0°, 10°S, 25°-30°S. Latitude 10°N delimits the northern distribution of not only *N. microps* and *N. tenella* but also other euphausiid species such as *Euphausia tenera, Thysanopoda monacantha, T. tricuspidata, Nematobrachion flexipes, Stylocheiron abbreviatum*, and *S. longicorne* (Brinton and Gopalakrishnan, 1973). Therefore, the Arabian Sea and Bay of Bengal north of lat. 10°N contains large numbers of only *N. gracilis* old form along with *Stylocheiron indicum, S. carinatum, S. affine, Pseudeuphausia latifrons, Euphausia diomediae*, and *E. distinguenda*. In both the Arabian Sea and the Bay of Bengal a low level of oxygen (as low as 0.1 ml/l) persists year-round in the upper oxygen minimum layer (Wyrtki, 1971). However, temperature and salinity vary seasonally in these areas. The surface salinity ranges are 30-33‰ for the Bay of Bengal and 34-37‰ for the Arabian Sea. Biologi-

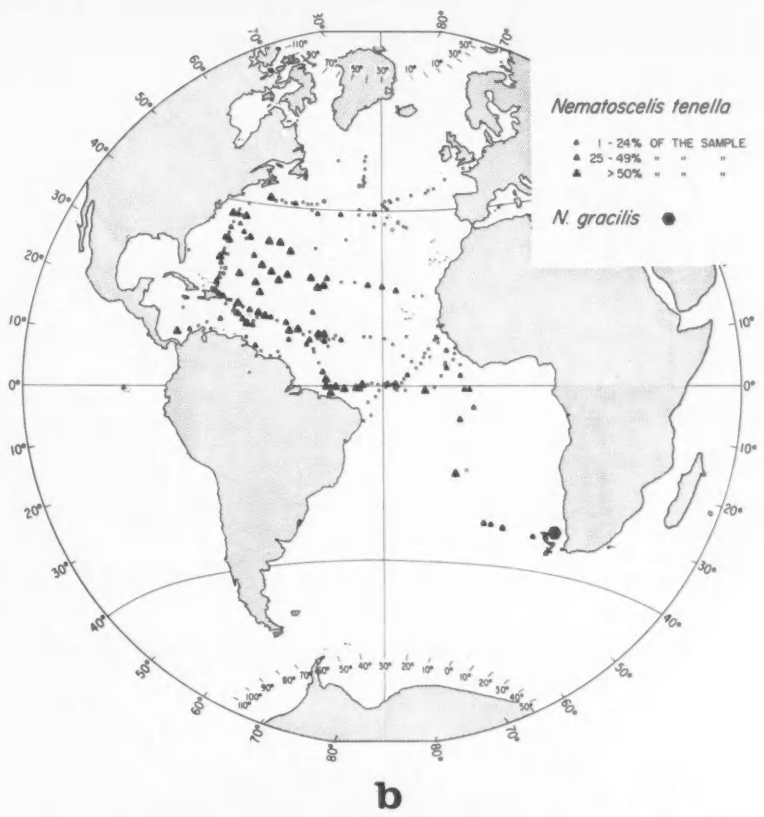

FIGURE 14.—Distribution of *Nematoscelis* in the Atlantic Ocean based on plankton samples: b - *N. tenella* and *N. gracilis*.

cal and oceanographical differences between these two parts of the Indian Ocean were discussed by Panikkar and Jayaraman (1966). Throughout the year *N. gracilis* old form maintains spawning populations in these two areas.

Nematoscelis gracilis new and old forms, *N. microps*, and *N. tenella* are part of the faunistic assemblage between lat. 0° and 10°S. The occurrence of *N. gracilis* new form in the mid-Pacific agrees with the distribution of *Euphausia pseudogibba* and *Thysanopoda subaequalis* in the zone lat. 10°-20°S (cf. Brinton, 1962:212). South of lat. 25°-30°S, *N. gracilis* is replaced by *N. atlantica*. Other species of this zone are *Euphausia brevis*, *E. mutica*, *Stylocheiron suhmii*, and *Thysanopoda subaequalis*. In the Indian Ocean all of these central species, including *N. atlantica*, occur only in the Southern Hemisphere.

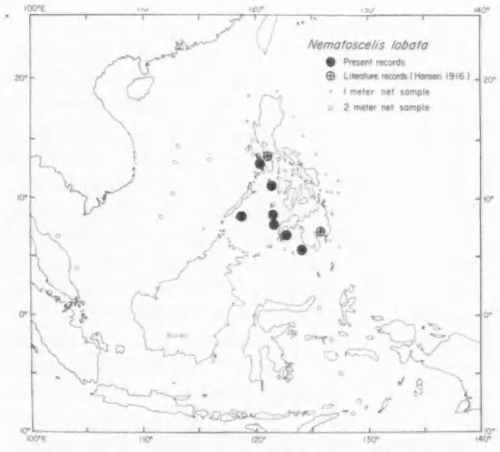

FIGURE 15.—All known records of *Nematoscelis lobata*.

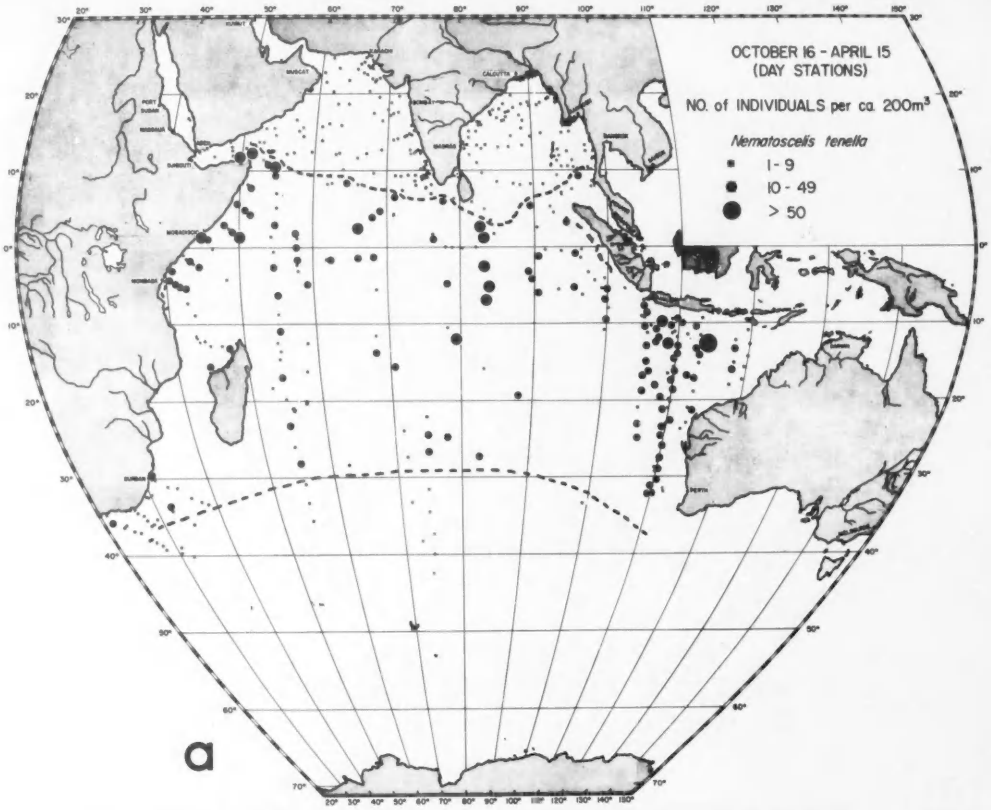

FIGURE 16.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis tenella* in the Indian Ocean: a - NE Monsoon period.

The distributions of *N. gracilis* new and old forms in the Indian and Pacific oceans appear respectively to be associated with areas of high and low oxygen concentration in the water column. In the Indian Ocean, Gibbs and Hurwitz (1967) reported a similar association of species distribution and oxygen concentration in the water column for two mesopelagic fish species, *Chauliodus pammelas* and *C. sloani*. Like *N. gracilis* old form, *C. pammelas* is only in the oxygen-poor waters of the Arabian Sea and the Bay of Bengal. The old form is largely confined to the tropical areas where the oxygen concentration in the upper minimum is less than 2 ml/l (Figure 3); whereas the new form occurs in those equatorial regions where the oxygen values in the upper minimum layer is never less than 1 ml/l. Since the adults have to pass through the oxygen minimum layer during their diurnal migrations, the old forms might have attained physiological adaptations to the lower oxygen levels. It has been documented experimentally (Teal and Carey, 1967) that *Euphausia mucronata*, one of the common residents in the oxygen-poor waters of the Peru-Chile Current, can withstand the stress of oxygen pressure as low as that in the oxygen minimum layer.

Low oxygen values in the upper minimum layer of the tropical Indian and Pacific oceans reflect the presumed high productivity of the surface layers (Vinogradov and Voronina, 1961; Longhurst, 1967). Old forms occur in these areas of high zooplankton abundance, particularly in the eastern tropical Pacific, Arabian Sea, and Bay of Bengal. Reid (1962) plotted the distribution of zooplankton abundance in the Pacific. In the area of the North Equatorial Current the zooplankton biomass is

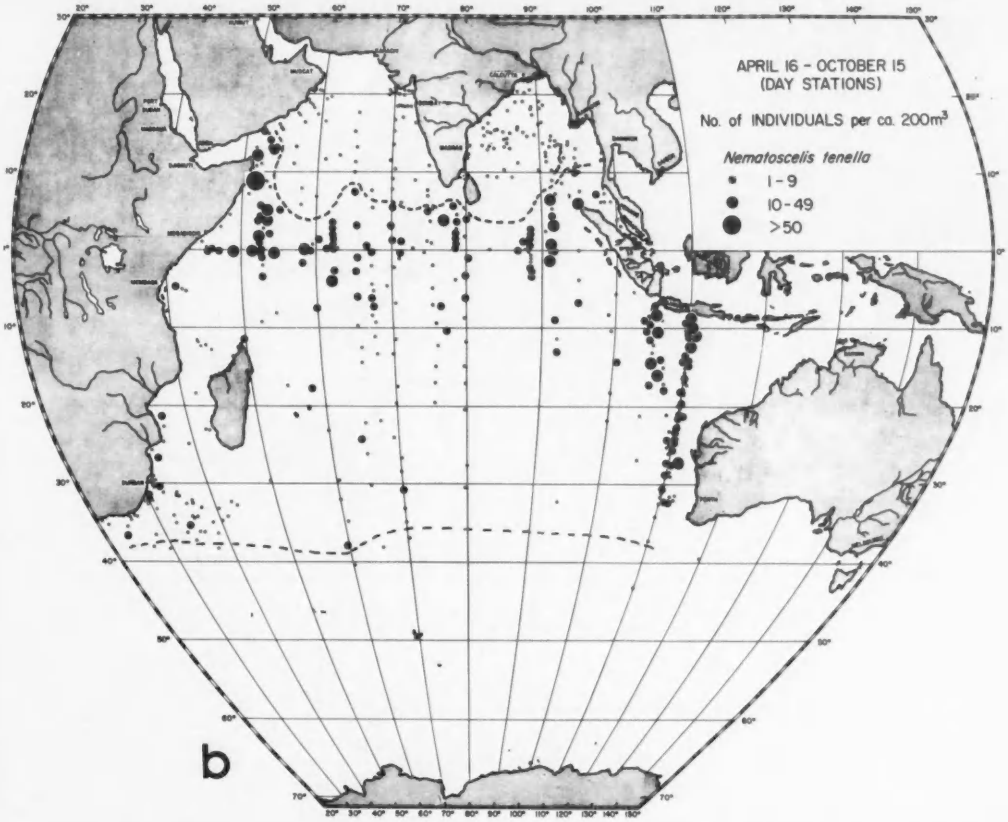

FIGURE 16.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis tenella* in the Indian Ocean: b - SW Monsoon period.

much higher than in the area of the South Equatorial Current. Correspondingly, *N. gracilis* old forms are distributed in the northern part of the equatorial current systems and new forms to the south in less rich waters. The same relationship exists in the Indian Ocean [cf. the International Indian Ocean Expedition Plankton Atlas. Indian Ocean Biological Centre (1968)].

Each form of *N. gracilis* is considered to be an ecophenotype. Mayr (1971) recognized ecophenotype as a nongenetic modification of the phenotype in response to an environmental condition. However, the observed morphological differences, associated with reproductive structures, suggest the possibility of genetic divergence of the two demes. The intergradation (intermediate forms) along the overlapping zones suggest incomplete genetic isolation.

Nematoscelis gracilis old forms in the northern part of the Indian Ocean differ from those of the eastern tropical Pacific in that the Indian Ocean forms are smaller in size. The degree of similarity of these two populations is expressed quantitatively in a separate paper.

Brinton (1962) pointed out that most of the inter-ocean waterways in the Indo-Australian Archipelago, (e.g., the Strait of Malacca, Sunda Strait, and Torres Strait) are too shallow (<100 m) to allow interoceanic transport of the oceanic euphausiid species. The deep pathway is through the straits of Molucca and Halmahera, and the Banda and Timor seas. Even central species like *Euphausia mutica* are found along this route. *Nematoscelis gracilis* new and old forms, *N. microps*, and *N. tenella* show similar communication between Pacific and Indian Ocean populations.

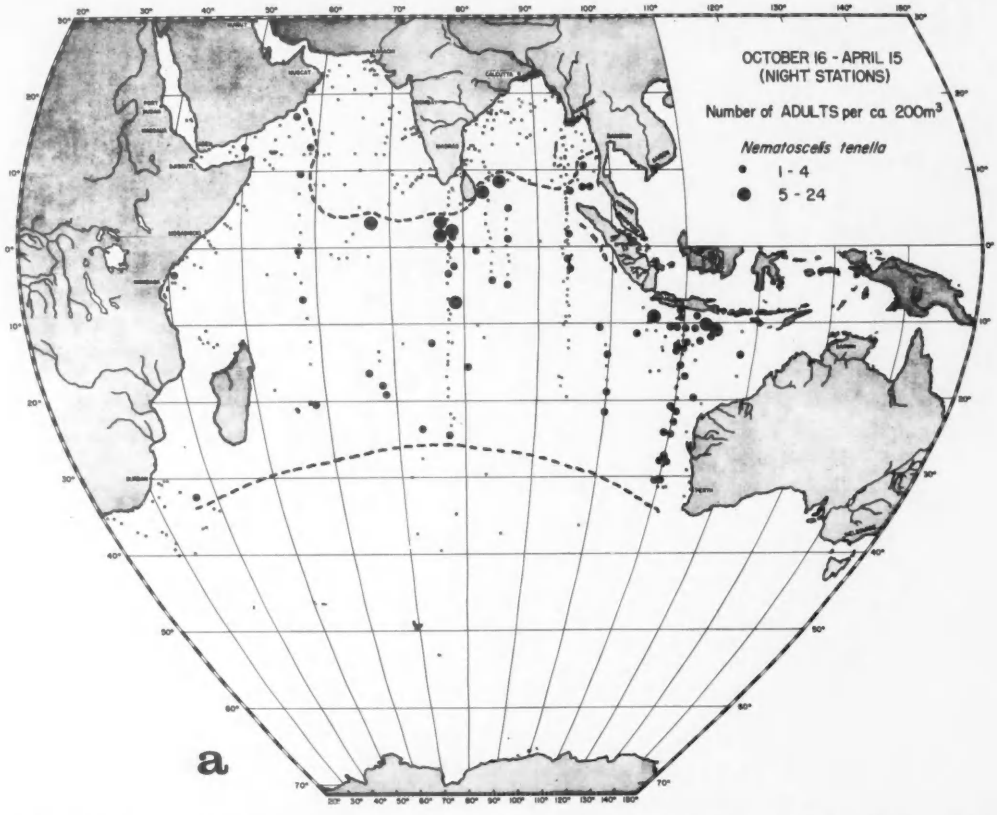

FIGURE 17.—Locality records and nighttime abundance of *Nematoscelis tenella* adults in the Indian Ocean: a - NE Monsoon period.

However, the absence of *N. atlantica* from the region of the Indo-Australian Archipelago suggests the lack of inter-ocean communication of this species. Moreover, *N. lobata,* which is morphologically most similar to *N. atlantica,* is endemic to a part of this region, mainly the Sulu and Celebes seas. These basins are connected with the open ocean by relatively shallow channels. This region is well known for its endemic species. Gilbert and Hubbs (1920) pointed out that the peculiar characteristics of the isolated basin of the Sulu Sea might have caused the evolution of many fish species. Because of morphological similarities and non-overlapping distribution (geographical isolation), *N. lobata* and *N. atlantica* may have derived from the same stock.

The North Pacific central population of *N. atlantica* is also isolated from its southern counterpart. However, it is not known whether the disjuncts are genetically different. Analyses performed by both numerical and conventional ways indicate no morphological differences.

Another region of importance in considering gene flow between Indian and Pacific populations is the South Australian Basin and the Tasman Sea. The Bass Strait between Australia and Tasmania is probably too shallow to allow passage of adult oceanic euphausiids. However, larvae and juveniles may be transported across this passage. The only route for adults is south of Tasmania, but this is almost certainly too far south for the tropical-subtropical species including *N. tenella, N. microps,* and *N. atlantica.* Evidence from south of Australia (Monsoon Expedition, long. 120°E-175°W) indicates that populations of *N. megalops* are in communication between the South Pacific and Indian oceans. The Pacific population evidently does not mix with the South At-

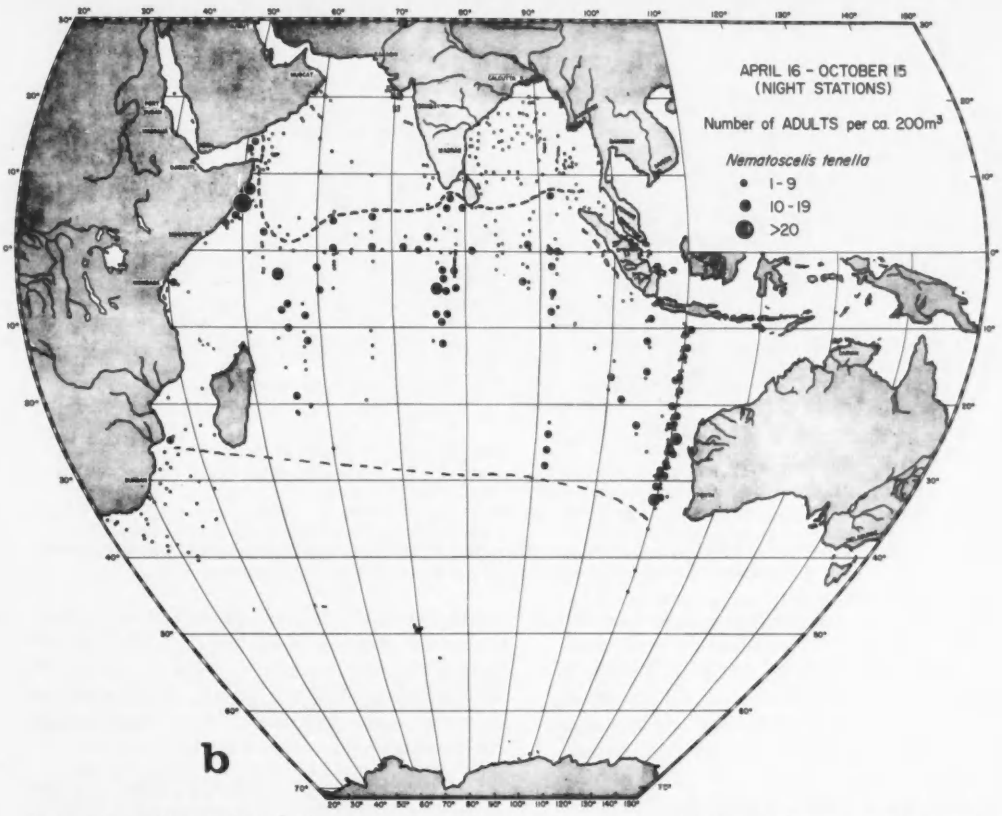

FIGURE 17.—Locality records and nighttime abundance of *Nematoscelis tenella* adults in the Indian Ocean: b - SW Monsoon period.

lantic counterpart at the Drake Passage (Antezana, manuscript). The morphological differences between *N. megalops* and *N. difficilis* already reflect presumed genetic differences.

Atlantic populations of *N. atlantica*, *N. microps*, and *N. tenella* are not in direct communication with their respective counterparts in the Pacific, but the North and South Atlantic populations are in communication at the Equator. It appears that the Atlantic and Indian Ocean populations of these species are in at least seasonal communication around the tip of South Africa.

A further aspect of the zoogeography of *Nematoscelis* in the Atlantic lies in the fact that *N. atlantica*, not *N. gracilis*, occupies the equatorial belt, permitting north-south continuity of the species. Atlantic expatriates of *N. gracilis* new form are found only off southwest Africa, probably transported by the Mozambique Current. The cool Benguela Current region may then limit northern transport of this tropical form, or the low oxygen (0.5 ml/l) in the minimum layer of the current, lat. 10°S and 15°S (Bubnov, 1966), might be a barrier to the new forms as it appears to be in the northern Indian Ocean.

There are similarities between distributions of species of *Nematoscelis* and those of other zooplankters. For example, the distribution of *N. megalops* is like that of a copepod, *Clausocalanus ingens* (Frost, 1969) and *Thysanoessa gregaria* (Brinton, 1962); horizontal boundaries of *N. microps* and *N. tenella* are like those of other tropical-subtropical species, *C. mastigophorus* and *Stylocheiron carinatum*. It is likely that both biological (species interaction) and physical [water mass, Sverdrup et al. (1942)] reasons are responsible for the numerous similarities.

McGowan (1971) classified the patterns of dis-

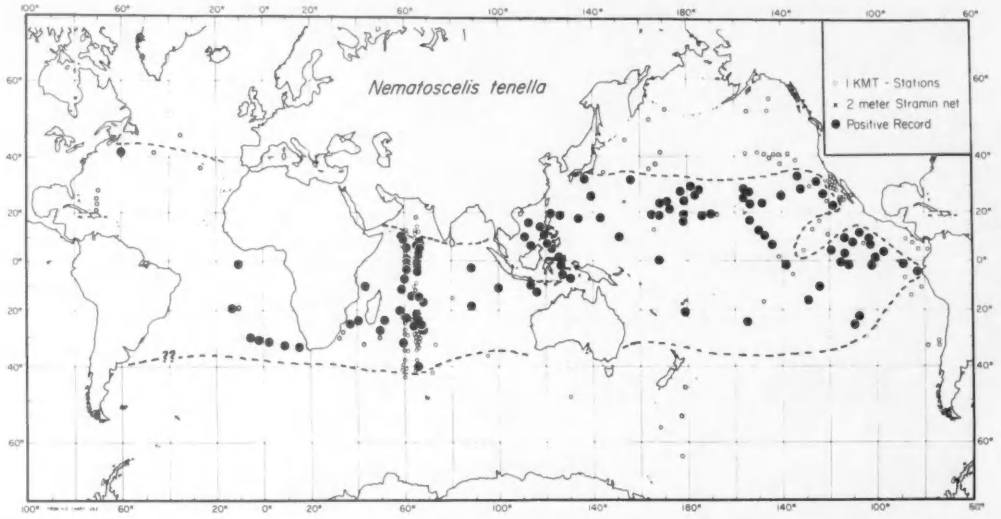

FIGURE 18.—Worldwide distribution of *Nematoscelis tenella* based on mid-water trawls. (Broken lines represent approximate boundaries of distribution of the species based on literature records and present evidence.)

tribution of many zooplankton species into four types on the basis of their association with water masses. They are: 1) species that show patterns of distribution whose boundaries are almost identical with the boundaries of the physical water masses; 2) species which have areas of highest levels of abundance within a water mass, but whose boundaries extend somewhat beyond the boundary of the water mass; 3) species that have distributions throughout several water masses; and 4) species having limited distributions in parts of some water masses. *Nematoscelis gracilis* and *N. atlantica* fall in the first category, *N. megalops* in the second, and *N. tenella* and *N. microps* in the third. *Nematoscelis difficilis* is restricted to the North Pacific transition zone whereas *N. megalops* is distributed in the central, transitional, and subarctic water masses of the Atlantic and in the southern transitional zones of the Indian and Pacific oceans.

ACKNOWLEDGMENTS

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VARIATION OF THE SURFACE GEOSTROPHIC FLOW IN THE EASTERN INTERTROPICAL PACIFIC OCEAN

MIZUKI TSUCHIYA[1]

ABSTRACT

A sequence of seven maps is presented to show the distribution of geopotential anomaly at the sea surface in the eastern intertropical Pacific Ocean. Each map represents a 2-mo period during the EASTROPAC expedition from February 1967 to April 1968.

The most striking feature revealed by these maps is the variation of the North Equatorial Countercurrent in response to the annual variation of the atmospheric circulation. In February-April (both 1967 and 1968), when the atmospheric intertropical convergence zone (ITCZ) lay near its southernmost position at lat. 2°-6°N, the Countercurrent was discontinuous and was rapidly changing in intensity. In August-September, when the ITCZ lay near its northernmost position at lat. 11°-15°N, the Countercurrent was strong, broad, and extended east all the way to the coast of Costa Rica.

In southern summer a weak and narrow eastward current was indicated along about lat. 10°S between long. 112° and 90°W within the westward flow of the South Equatorial Current. This current is so weak that it is probably buried in the westward Ekman drift due to the southeast trades and can be observed only when the trade winds are unusually weak.

An eastward current, which can be interpreted as the Equatorial Undercurrent breaking the sea surface, was indicated within about 2° of the equator in April-May, when the southeast trades were relatively weak near the equator.

The distributions of relative geostrophic flow in February-March 1967 and February-April 1968 were remarkably similar over the entire study area.

The purpose of this paper is to present a sequence of seven maps (Figures 1-7) showing the distribution of geopotential anomaly at the sea surface of the eastern intertropical Pacific Ocean from February 1967 to April 1968 and to discuss the variations of the circulation revealed by these maps. Each map represents a 2-mo period during the EASTROPAC expedition, which was an international cooperative oceanographic investigation coordinated by the Bureau of Commercial Fisheries (now National Marine Fisheries Service).

Prior to EASTROPAC a considerable number of expeditions took place in the eastern intertropical Pacific Ocean; consequently, its principal oceanographic features were reasonably well known (e.g., Wooster and Cromwell, 1958; Bennett, 1963; Wyrtki, 1966, 1967; Tsuchiya, 1968; Stroup, 1969). However, the accumulated data were too sparse in time and space to give insight into monthly or seasonal variations in the distribution of oceanographic properties. The EASTROPAC expedition was designed to acquire data to bring to light these time variations.

[1]Institute of Marine Resources, Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92037.

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The expedition was divided into seven 2-mo cruise periods. During each period, a single-ship or multiship cruise was carried out. Multiship cruises took place in February-March, August-September 1967, and February-April 1968. These cruises covered the area between lat. 20°N and 20°S (15°S in August-September 1967) and from the coast of the American continents westward to long. 119°W (126°W in February-March 1967). Single-ship cruises took place in April-May, June-July, October-November 1967, and December 1967-January 1968 in time intervals between the multiship cruise periods. Each of these cruises covered the area between lat. 20°N and 3°S and between long. 98° and 119°W.

Details of the observational program, the list of participating vessels, and track charts have been published in the EASTROPAC atlas (Love, 1972a).

DATA

Almost all EASTROPAC stations with observations to 500 m or deeper were used in this study. These stations are listed in Table 1 and can be identified on the track charts included in the EASTROPAC atlas (Love, 1972a).

TABLE 1.—List of stations used in Figures 1-7.

Ship and cruise	Stations	Dates	Number of stations used	Data type[1]	Figure number
Argo 11	2, 25-328	25 Jan.-2 Mar. 1967	152	a	Fig. 1
Jordan 12	2-284	12 Feb.-21 Mar. 1967	129	a	
Rockaway 13	1-265, 318-342	1 Feb.-20 Mar. 1967	129	b	
Alaminos 14	1-101, 110-159, 194-267, 301, 309, 332, 333, 340-342	31 Jan.-3 Apr. 1967	143 Total 553	a, b	
Jordan 20	5-264	13 Apr.-24 May 1967	129	a	Fig. 2
Jordan 30	8-264	17 June-27 July 1967	149	a, c	Fig. 3
Washington 45	7-206, 282-387	6 Aug.-15 Sept. 1967	177	a	Fig. 4
Undaunted 46	2-189	16 Aug.-22 Sept. 1967	141	a	
Rockaway 47	1-40, 49-113, 124-258, 268-382, 402-527	1 Aug.-23 Sept. 1967	212 Total 530	b	
Jordan 50	5-249	20 Oct.-26 Nov. 1967	126	a	Fig. 5
Jordan 60	2-289	21 Dec. 1967-28 Jan. 1968	166	a	Fig. 6
Washington 75	1-144, 187-258	18 Feb.-8 Apr. 1968	160	a	Fig. 7
Jordan 76	1-255	21 Feb.-30 Mar. 1968	131	a	
Rockaway 77	6-103, 113-278, 302-438, 475-571	30 Jan.-18 Apr. 1968	263 Total 554	b	

[1]a: STD digital data logger; b: STD analogue charts; c: Nansen-bottle casts.

Temperature and salinity data used for computing geopotential anomaly were collected with in situ salinity-temperature-depth recorders (STD) except for those from EASTROPAC cruise *David Starr Jordan* 30, on which a breakdown of the STD necessitated the use of Nansen bottles during the last half of the cruise. Most of the STD data were obtained from digital data loggers, but some were digitized from analogue charts (Table 1). The method of processing STD data is described in the EASTROPAC atlas (Love, 1972a).

From these temperature and salinity data, geopotential anomaly at the sea surface was computed with reference to 500 db. Because of relatively homogeneous water at depths greater than 500 m in the intertropical ocean, this reference is believed to be adequately deep for estimating the geostrophic current at the sea surface. The unit of geopotential anomaly is chosen to be joule per kilogram (abbreviated J/kg; equivalent to dynamic decimeter).

Computed geopotential anomaly was plotted on each map, and smooth isopleths were drawn at intervals of 1.0 or 0.5 J/kg. The base map is a Mercator projection and was adapted from U.S. Navy H. O. 526 and 823.

THE SURFACE GEOSTROPHIC FLOW

The surface geostrophic flow revealed by the maps of geopotential anomaly is described below. A comparison of these maps with other maps based on long-term averages of set and drift of ships is also made. The atlas of the monthly average surface currents in the eastern North Pacific published by the U.S. Navy Hydrographic Office (H. O. 570, 1947) and the atlas of the quarterly average surface currents in the South Pacific published by the Meteorological Office (M. O. 435, 1939) are pertinent to the comparison. There are also monthly drift charts by Cromwell and Bennett (1959) for the northern hemisphere and those by Puls (1895) and Wyrtki (1965) for both hemispheres. The charts by Cromwell and Bennett are simply a different presentation of the H. O. 570 charts for the area east of long. 120°W and south of lat. 30°N. Puls' charts show the current direction and relative intensity for the area between lat. 20°N and 10°S. Wyrtki's charts are based on averages over 1-degree squares, but it is not clear how he smoothed or interpolated the original 1-degree averages to obtain the current patterns shown on his charts.

Various sources of errors and disparities in the geostrophic calculation and set-and-drift observations should be kept in mind. Geopotential anomaly computed from oceanographic data may include short-period density fluctuations that are not necessarily associated with fluctuations of the actual current. The calculation of geostrophic flow neglects the direct frictional effect of wind stress.

On the other hand, set-and-drift observations are affected by strong winds, sea, swell, and tidal currents.

South Equatorial Current Region

The South Equatorial Current is well defined west of long. 90°W on the maps for February-March 1967, August-September 1967, and February-April 1968 (Figures 1, 4, and 7). South of lat. 10°S the direction of geostrophic flow is predominantly to the northwest, whereas the drift charts (Meteorological Office, 1939; Wyrtki, 1965) for the corresponding months indicate that the surface current flows almost due west in this region. This disagreement may be due to the effect of the Ekman drift. The trade winds in this area are from the southeast to east, so that if the Ekman drift is added to the geostrophic flow, the resultant surface current would be nearly to the west.

North of lat. 10°S the South Equatorial Current becomes more zonal and flows almost due west. In February-March 1967 (Figure 1) the westward flow of the South Equatorial Current extends across the equator to about lat. 5°N, and the current near the equator west of the Galápagos Islands is also westward. In April-May 1967 (Figure 2) the westward flow of the South Equatorial Current is interrupted by an eastward current within about 2° of the equator. Puls' (1895) charts of the surface current for March and April clearly show an eastward current at the equator between long. 110°W and the Galápagos Islands. Such an eastward current can be interpreted as the Equatorial Undercurrent breaking the sea surface during local weakening of the easterly trades (Cromwell, Montgomery, and Stroup, 1954; Montgomery, 1962; Montgomery and Stroup, 1962:59-60). Jones (1969) has presented evidence of a surfacing of the Undercurrent on the basis of direct current measurements made at long. 98°W in April 1968 (EASTROPAC cruise *Thomas Washington* 75). The distribution of geopotential anomaly from this cruise, however, does not suggest a surfacing of the Undercurrent (Figure 7).

On the other maps (Figures 3-7) flow is westward from the equator to about lat. 5°N, and in some longitudes an eastward current is revealed just south of the equator, because geopotential anomaly does not show a minimum at the equator but a few degrees of latitude south of the equator. The same distribution of geopotential anomaly can be seen on Bennett's (1963, Figure 6) map based on EASTROPIC data. This distribution is associated with a thermocline ridge that tends to occur at lat. 1°-3°S (instead of the equator) in the eastern Pacific. This southward displacement of the ridge from the equator is clearly evident on many of EASTROPAC vertical sections of temperature or thermosteric anomaly and maps of the topography of the 300-cl/t isanosteric surface, which lies close to the center of the thermocline (Love, 1971, 1972b, 1973, in press). According to Cromwell's (1953) simple model of the wind-driven meridional circulation, the direction of the wind near the equator determines the position of the maximum divergence of the Ekman transport in the surface layer. He points out that the meridional component of the southeast trades shifts the maximum divergence, which would correspond to a ridge of the thermocline, to the south of the equator.

The eastward geostrophic flow between the equator and the ridge was first discussed by Austin (1960) and later commented upon by Stroup (1969:35). It is not certain, however, that the actual surface current is eastward south of the equator. Estimates of the magnitudes of terms in the equation of motion suggest that the southward pressure gradient is in approximate balance with the northward component of wind stress. The M. O. 435 drift chart for the May-July quarter shows very weak easterly components just south of the equator at long. 100°-110°W between strong westward currents to the north and south. The drift charts for the other quarters show no evidence of an eastward current south of the equator.

The southern-summer maps (Figures 1 and 7) exhibit a weak eastward current along about lat. 10°S from long. 112°W to about 90°W. Examination of vertical sections of temperature and maps of surface temperature in the EASTROPAC atlas (Love, 1972a, in press) indicates that this current is associated with a slight southward shoaling of a shallow summer thermocline and with a meridional temperature gradient developed during summer between a pool of warm surface water south of the equator and cold surface water farther south that appears to be coming from the Chile Current (Wooster, 1970). This suggests that the eastward geostrophic current along lat. 10°S is found only in southern summer. (It is interesting to note that the North Equatorial Countercurrent, which flows east at roughly the same latitude in the northern hemisphere, is most strongly developed during the same season, i.e., northern

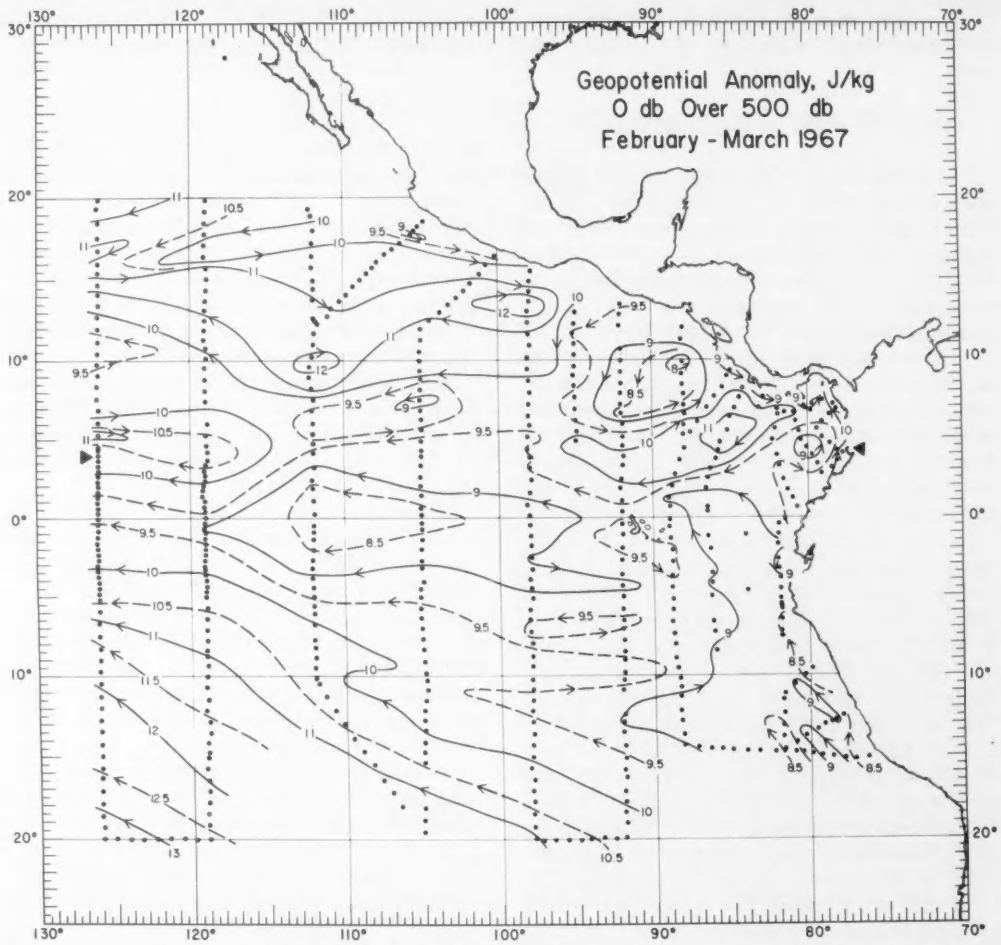

FIGURE 1.—Geopotential anomaly, in joules per kilogram (dynamic decimeters), at the sea surface relative to 500 db in February-March 1967. EASTROPAC cruises *Argo* 11, *David Starr Jordan* 12, *Rockaway* 13, and *Alaminos* 14. The position of the intertropical convergence zone at the eastern and western ends of the map is indicated by triangles.

summer.) However, the coverage of the southern-winter map (Figure 4) is limited to lat. 10°S, and this suggestion cannot be confirmed by winter data. None of the drift charts examined shows an eastward current near this latitude in the eastern South Pacific, but their data are too sparse to draw a definite conclusion. Because of its low speed, the countercurrent, indicated by the distribution of geopotential anomaly (Figures 1 and 7), may well be buried in the westward Ekman drift due to the prevailing southeasterly trades and may be observed only when the trade winds are unusually weak.

Peru Current

In the region south of the equator and between long. 90°W and the coast of South America, the distribution of geopotential anomaly is irregular, and its spatial variation is not large (Figures 1, 4, and 7). This distribution suggests a dominance of weak and broad flow with small-scale irregularities such as eddies and countercurrents (Wooster and Reid, 1963; Wyrtki, 1963). Partly because of this fact and partly because of a rather inadequate orientation of ship tracks in this area, contouring is difficult; there are many other ways

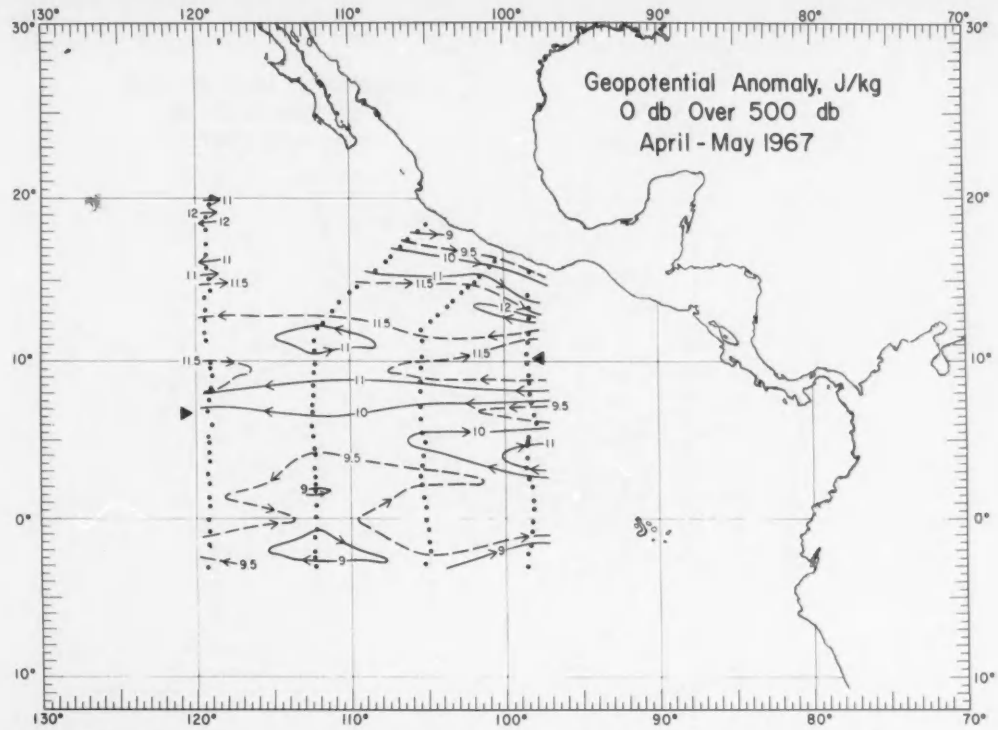

FIGURE 2.—Geopotential anomaly, in joules per kilogram (dynamic decimeters), at the sea surface relative to 500 db in April-May 1967. EASTROPAC cruise, *David Starr Jordan* 20. The position of the intertropical convergence zone at the eastern and western ends of the map is indicated by triangles.

to draw isopleths. Consequently, the deduced geostrophic-flow pattern is not everywhere reliable. Nevertheless, the general trend of flow indicated by the present maps is parallel to the coast and toward the equator. There is not much change in general flow patterns during the EASTROPAC period.

Eastern Boundary Currents in the Northern Hemisphere

In this region flow also tends to follow the coastline. On the map for February-March 1967 (Figure 1), there is an indication of a northward current, the Colombia Current (Wooster, 1959; Stevenson, 1970), flowing close to the coast of Colombia toward the Gulf of Panama. On the maps for August-September 1967 and February-April 1968 (Figures 4 and 7) the distribution of stations is inadequate for defining the Colombia Current.

Off Costa Rica the direction of flow varies, depending on the development of an anticyclonic eddy farther offshore. The strong southeastward flow indicated by the map for February-March 1967 (Figure 1) is associated with the northern edge of an anticyclonic eddy centered at lat. 5°N, long. 85°W. A similar anticyclonic eddy is observed in February-April 1968 (Figure 7), but is centered at lat. 5°N, long. 88°W, farther west than in 1967; and the flow near the coast of Costa Rica is northwestward. As Puls (1895:24 and 27), Cromwell (1958), and Wyrtki (1965) have noted, their drift charts also show a well-developed anticyclonic eddy in this area from February to March. This anticyclonic eddy seems to be a normal feature in these months. In August-September (Figure 4), when no such anticyclonic eddy develops, the area off the coast of Costa Rica is dominated by the northwestward return flow of the North Equatorial Countercurrent.

A cyclonic circulation is well developed around the Costa Rica thermal dome centered near lat.

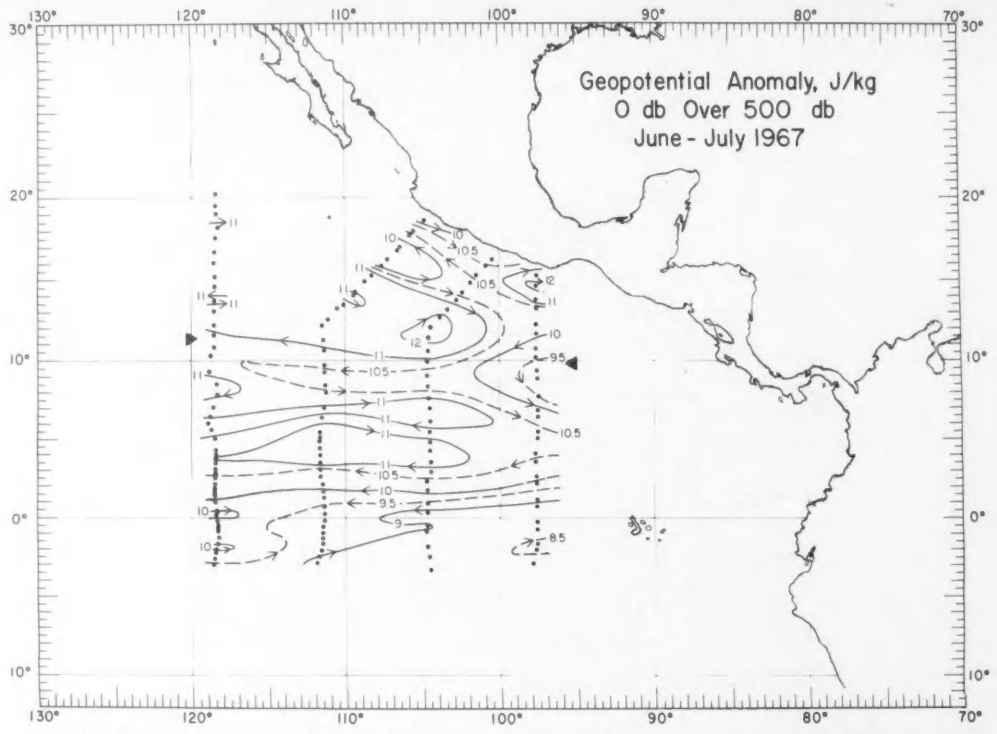

FIGURE 3.—Geopotential anomaly, in joules per kilogram (dynamic decimeters), at the sea surface relative to 500 db in June-July 1967. EASTROPAC cruise *David Starr Jordan* 30. The position of the intertropical convergence zone at the eastern and western ends of the map is indicated by triangles.

9°N, long. 89°W (Brandhorst, 1958; Cromwell, 1958; Wooster and Cromwell, 1958; Wyrtki, 1964) in February-March 1967 and February-April 1968 (Figures 1 and 7), but is less well defined in August-September 1967 (Figure 4).

Between Costa Rica and Cape Corrientes (lat. 20°N), nearshore flow is generally northwestward in August-September (Figure 4), when the North Equatorial Countercurrent is strongly developed. In the other months (Figures 1-3 and 5-7) flow is southeastward from Cape Corrientes at least as far south as the Gulf of Tehuantepec (lat. 16°N). This sense of flow is in agreement with that found on the H. O. 570 drift charts except for June-July, when the nearshore current is northwestward on the drift charts. Puls' (1895) charts, however, indicate easterly components of flow near the coast between Cape Corrientes and the Gulf of Tehuantepec in all months of the year.

North Equatorial Countercurrent

Previous studies (e.g., Wyrtki, 1965) have indicated that the North Equatorial Countercurrent is subject to a large variation in response to that of the atmospheric circulation, particularly the annual meridional migration of the intertropical convergence zone (ITCZ). During EASTROPAC the North Equatorial Countercurrent exhibited a high level of variability in position and intensity. The Countercurrent was weak and discontinuous in February-April 1967 and 1968, when the ITCZ lay near its southernmost position at lat. 2°-6°N. It was strong, broad, and extended all the way to the coast of Costa Rica in August-September 1967, when the ITCZ lay near its northernmost position at lat. 11°-15°N. (The position of the ITCZ during EASTROPAC can be inferred from surface-wind charts in the EASTROPAC atlas.

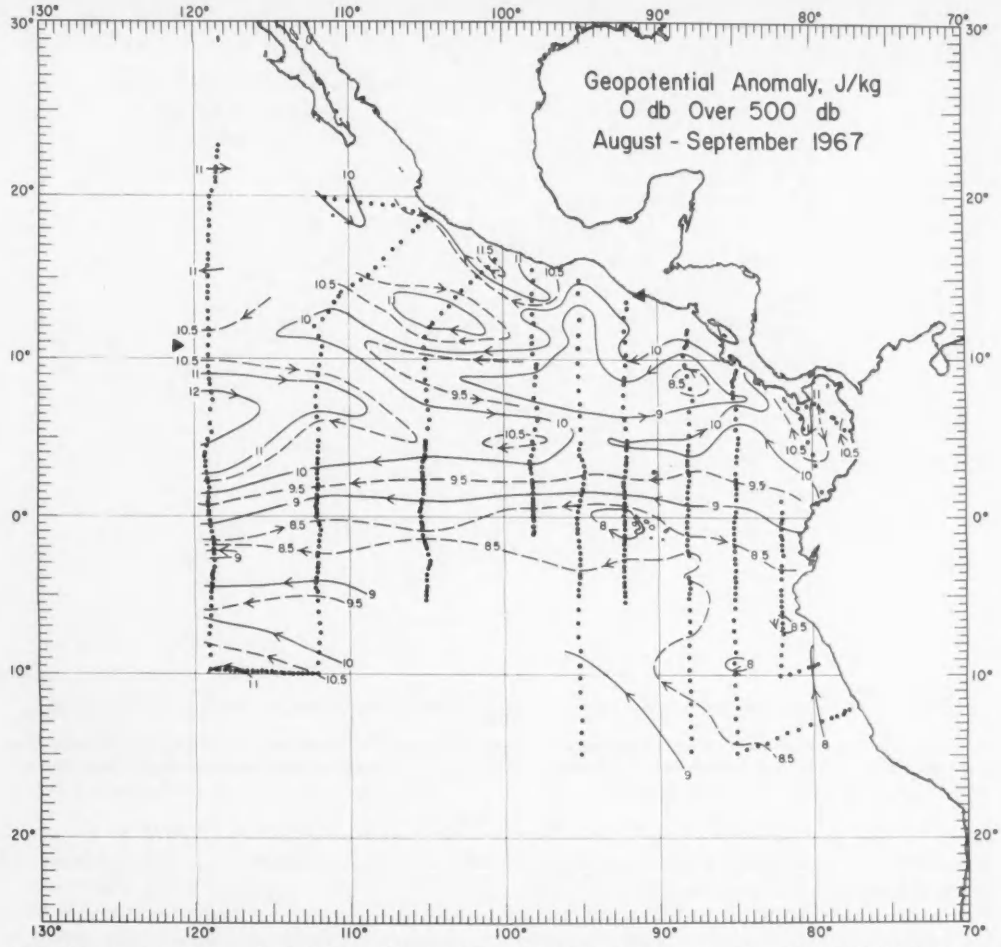

FIGURE 4.—Geopotential anomaly, in joules per kilogram (dynamic decimeters), at the sea surface relative to 500 db in August-September 1967. EASTROPAC cruises *Thomas Washington* 45, *Undaunted* 46, and *Rockaway* 47. The position of the intertropical convergence zone at the eastern and western ends of the map is indicated by triangles.

The position at the easternmost and westernmost meridional sections is indicated by triangles on each map in Figures 1-7.)

In February-March 1967 (Figure 1) the North Equatorial Countercurrent is present between lat. 5° and 8°N[2] at long. 126° and 119°W, but it is practically missing at long. 112°W and only weakly developed at long. 105°W. At long. 98°W the Countercurrent is entirely absent. From long. 95° to 85°W a strong eastward current, which can be identified as the North Equatorial Countercurrent, is found along lat. 5°-6°N between the cyclonic and anticyclonic eddies mentioned earlier. In April-May (Figure 2) no countercurrent is found at long. 119°, 112°, and 105°W, but a strong countercurrent is indicated between lat. 4° and 7°N at long. 98°W. In April-May the ITCZ starts returning to the north and is located north of lat. 6°N.

The development of the North Equatorial Countercurrent in February-April 1968 (Figure

[2]Near the northern edge of the North Equatorial Countercurrent, flow is usually weak, and the current boundary is not always well defined by the distribution of geopotential anomaly. The northern boundary cited here is that of the band of strong current. Weak eastward flow may extend farther north.

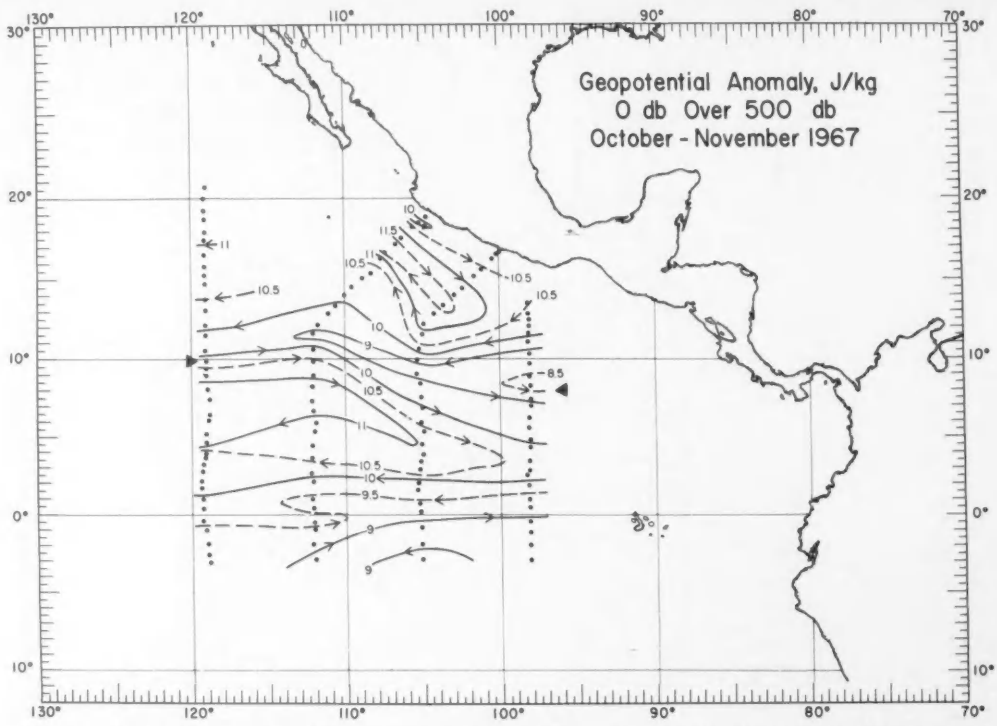

FIGURE 5.—Geopotential anomaly, in joules per kilogram (dynamic decimeters), at the sea surface relative to 500 db in October-November 1967. EASTROPAC cruise *David Starr Jordan* 50. The position of the intertropical convergence zone at the eastern and western ends of the map is indicated by triangles.

7) is much like that in February-April 1967 (Figure 1). In 1968 the Countercurrent is present between lat. 4° and 7°N at long. 119°, 112°, and 105°W, but is not found at long. 98° and 95°W. Farther east at long. 88° and 85°W the Countercurrent is strongly developed along lat. 5°-8°N between cyclonic and anticyclonic eddies similar to those observed in 1967.

By June-July 1967 (Figure 3) the North Equatorial Countercurrent is well established between lat. 6° and 10°N on all four meridional sections. In Figure 3 a weak eastward current, separated from the Countercurrent by a narrow band of westward flow, can be seen about 200 km south of the southern boundary of the Countercurrent. This secondary countercurrent represents a surfacing of a narrow but stable subsurface eastward current, which has its maximum speed at a depth of 50-200 m just south of the North Equatorial Countercurrent (Tsuchiya, 1972).

In August-September (Figure 4) the North Equatorial Countercurrent is fully developed and extends east to the coast of Costa Rica, where it turns to the northwest along the coast. In these months the Countercurrent is wider and is located farther north than in the February-April periods of 1967 and 1968. In August-September it lies between lat. 7° and 11°N at long. 119° and 112°W and between lat. 5° and 10°N east of long. 105°W (Figure 4). About the same condition continues through November (Figure 5), although the ITCZ starts shifting south in October. In December-January (Figure 6) the Countercurrent starts moving south, following the ITCZ's southward shift, which began 2 mo earlier.

The variation of the North Equatorial Countercurrent revealed by the present maps of geopotential anomaly generally agrees with the results of set-and-drift observations discussed by Puls (1895), Cromwell and Bennett (1959), and Wyrtki (1965).

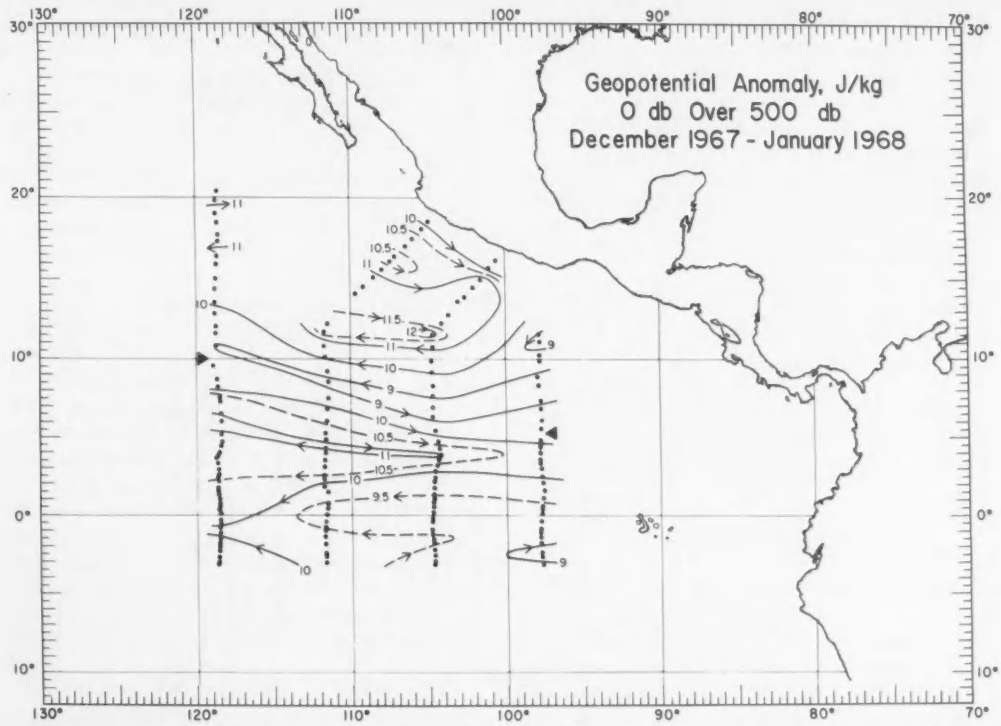

FIGURE 6.—Geopotential anomaly, in joules per kilogram (dynamic decimeters), at the sea surface relative to 500 db in December 1967-January 1968. EASTROPAC cruise *David Starr Jordan* 60. The position of the intertropical convergence zone at the eastern and western ends of the map is indicated by triangles.

North Equatorial Current Region

North of the North Equatorial Countercurrent, the North Equatorial Current is found on all seven maps (Figures 1-7). On the maps for February-March 1967 and February-April 1968 (Figures 1 and 7) the westward flow of the North Equatorial Current starts off the Gulf of Tehuantepec with a major contribution of water coming from the northwest along the Mexican coast. Water coming from the southeast appears to return to the east forming a cyclonic eddy around the Costa Rica thermal dome.

In February-March 1967 (Figure 1) the North Equatorial Current is interrupted by a continuous eastward flow indicated along lat. 15°N from long. 126°W to the coast of Mexico, where it turns to the south to feed the North Equatorial Current. This eastward flow is broadly developed at long. 112°W and extends from lat. 10° to 18°N. There is a suggestion that a similar eastward flow is present in April-May 1967 and February-April 1968 (Figures 2 and 7). Reid's (1961) map of the surface geostrophic flow also indicates an eastward current at about the same latitude from long. 130° to 95°W, but his data in this area are principally from northern fall and winter. The surface drift charts (Puls, 1895; U.S. Navy Hydrographic Office, 1947) do not show such an eastward flow west of long. 110°W, possibly because of the westward Ekman drift and leeway of ships due to the strong northeasterly trades.

On the map for August-September (Figure 4) the North Equatorial Current starts off the coast of Costa Rica. East of long. 100°W it is fed almost entirely by the return flow of the North Equatorial Countercurrent, which is fully developed in these months.

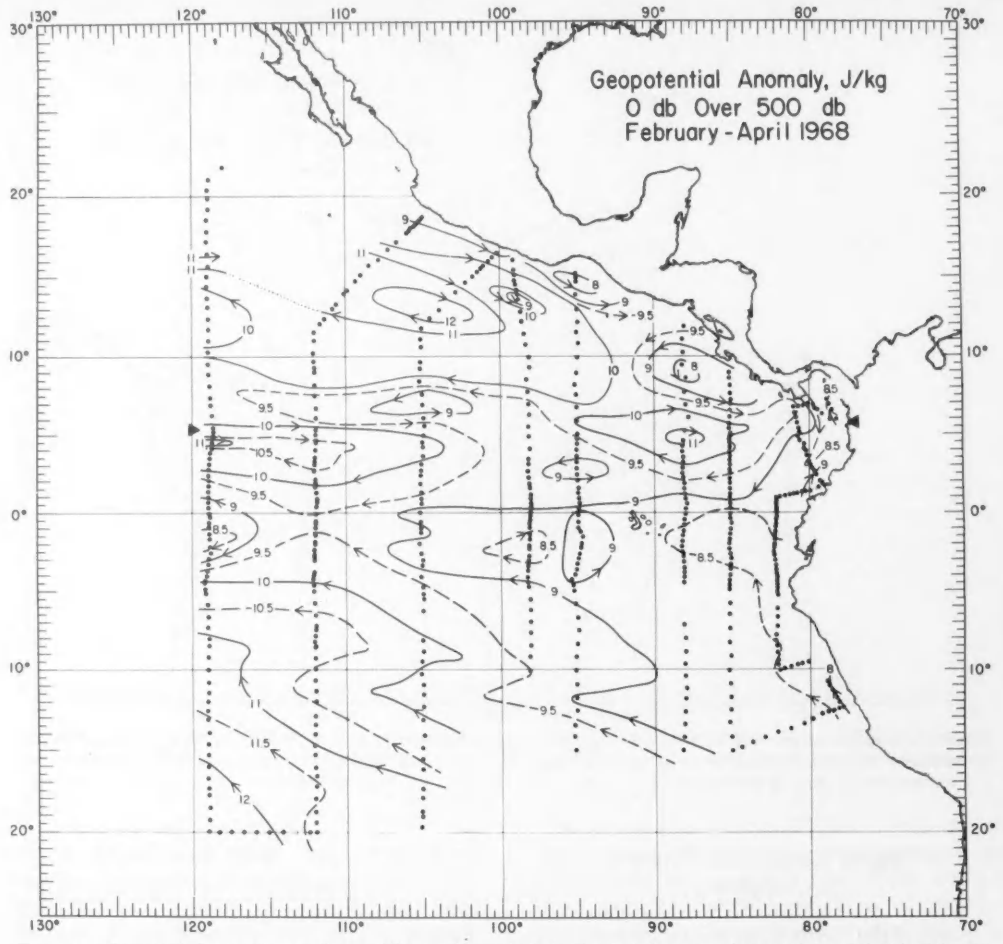

FIGURE 7.—Geopotential anomaly, in joules per kilogram (dynamic decimeters), at the sea surface relative to 500 db in February-April 1968. EASTROPAC cruises *Thomas Washington* 75, *David Starr Jordan* 76, and *Rockaway* 77. The position of the intertropical convergence zone at the eastern and western ends of the map is indicated by triangles.

DISCUSSION

As was noted earlier, geopotential anomaly computed from oceanographic data contains short-period nongeostrophic fluctuations of the mass field, but there is no way of removing them from the data. Consequently, not all of the features indicated by the present maps may be real. Despite this problem, EASTROPAC data are unique in their time and space coverage and in the close spacing of stations on tightly coordinated ship tracks and, thus, reveal some interesting features that have not been observed previously.

A zonal discontinuity of the North Equatorial Countercurrent in the months when the ITCZ lies near its southernmost position is suggested by the monthly average drift charts (U.S. Navy Hydrographic Office, 1947; Wyrtki, 1965); however, the present maps (Figures 1, 2, and 7) are the first to show it on the basis of quasi-synoptic oceanographic data from the entire eastern intertropical North Pacific. (It is highly unlikely that the breakup of the Countercurrent as shown on

these maps is an artifact of short-period fluctuations of the mass field.) In these months the Countercurrent shows a drastic change in intensity; its rapid disappearance and reappearance on this sequence of maps (Figures 1-3, 6, and 7) are remarkable. The maps demonstrate that the Countercurrent can either disintegrate or reestablish itself on a time scale less than 2 mo.

A comparison of the present maps (Figures 1-7) with meteorological charts in the EASTROPAC atlas (Love, 1971, 1972a, 1972b, 1973, in press. See also the position of the ITCZ indicated at the eastern and western ends of each map.) reveals a rather good correlation between the positions of the North Equatorial Countercurrent and the ITCZ. The northern boundary of the Countercurrent (minimum of geopotential anomaly) coincides approximately with the ITCZ except in February-March and August-September. In February-March the southern boundary of the Countercurrent, if it is present, more nearly coincides with the ITCZ; in August-September the ITCZ is located far to the north of the northern boundary. This finding is in agreement with what can be seen on Wyrtki's (1965) long-term average charts.

There is a high degree of similarity in geostrophic-flow patterns between February-March 1967 (Figure 1) and February-April 1968 (Figure 7). The major features are much the same for the two maps; even the development of the cyclonic and anticyclonic eddies off Costa Rica, the discontinuity of the North Equatorial Countercurrent near long. 98°W, and the eastward flow along about lat. 10°S are similar. In view of the large variations observed between the two cruise periods, this similarity is perhaps surprising. The only notable difference is the latitude of the minimum of geopotential anomaly near the equator (discussed in the preceding section) west of the Galápagos Islands; the minimum is located at the equator in 1967 (Figure 1), while it is located a few degrees south of the equator in 1968 (Figure 7). The southward shift of the minimum in Figure 7 is probably due to the more southerly trade winds near the equator in 1968 than in 1967 (Cromwell, 1953).

The eastward current indicated along about lat. 10°S on the southern-summer maps (Figures 1 and 7) is of particular interest, because no previous data from the eastern Pacific have suggested it. This countercurrent is very weak (the average geostrophic speed from seven meridional sections is 7 cm/s) and was not noticed in earlier examination of vertical sections based on EASTROPAC data (Tsuchiya, 1972). It is a narrow and thin current (about 50 m thick) and is completely separate from a subsurface eastward current which has its maximum speed at a depth of 70-200 m and which flows along about lat. 6°S (Stroup, 1969; Tsuchiya, 1972).[3] More data are needed to determine the relation of this surface eastward countercurrent with the South Equatorial Countercurrent, which is well developed near lat. 10°S at the sea surface of the central and western Pacific (Reid, 1959, 1961; Merle, Rotschi, and Voituriez, 1969; Rotschi, 1970; Tsuchiya, 1970; Donguy and Rotschi, 1970). As was mentioned in the preceding section, the former countercurrent is defined only between long. 112°W and long. 90°W and is not found in the west of the EASTROPAC area.

ACKNOWLEDGMENTS

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THERMOREGULATORY BEHAVIOR AND DIEL ACTIVITY PATTERNS OF BLUEGILL, *LEPOMIS MACROCHIRUS*, FOLLOWING THERMAL SHOCK

THOMAS L. BEITINGER[1]

ABSTRACT

Individual bluegill were allowed to thermoregulate for 3 days in a temperature-preference apparatus and then were exposed for 30 min to one of three temperature treatments: 21.0°, 31.0°, or 36.1°C. Fish exposed to 31°C served as controls for handling procedures. Thermoregulatory performance of surviving fish was monitored for an additional 3 days. Pretreatment results indicated mean lower and upper avoidance temperatures of 29.3° and 33.1°, and 31.2°C as the midpoint of the preferred range. All 20 fish exposed to 21° and 31°C survived treatment and demonstrated no significant differences between pretreatment and posttreatment thermoregulatory performance. Thirty-five percent of fish (7 of 20) exposed to 36.1°C died during treatment. Fish surviving the 36.1°C treatment retained the ability to thermoregulate; however, their mean lower and upper avoidance temperatures increased 0.6° and 0.7°C, respectively. Activity patterns were typically diurnal, but variable, in all three treatment groups. Immediately after treatment, the activity of fish exposed to 21° and 36.1°C was markedly decreased. Thereafter, activity tended to be higher in the 21°C group and lower in the 36.1°C group than during the pretreatment period.

Opportunities for temperature shock occur wherever sharp temperature gradients are present. Fish may be exposed to a sudden temperature change when penetrating the thermocline; in areas containing springs, upwellings or natural allochthonous inputs of water; in sharp horizontal temperature gradients characteristic of shallow waters; and during the passage of weatherfronts. Also, fish species migrating through or residing within waters under the influence of electric generating companies may be subjected to sudden temperature changes.

Investigations concerning thermal shock of fishes have mainly been limited to descriptions of morbidity stages and determinations of species' lethal temperatures. Noteworthy exceptions are studies by Sylvester (1972) and Coutant (1972a, b, 1973) that demonstrate enhanced vulnerability of thermally stressed fishes to predation. Fish mortalities owing to natural and artificially induced temperature shock have been reported in marine, estuarine, and freshwater environments (Gunther, 1936; Gunter, 1941; Huntsman, 1942; Gunter and Hildebrand, 1951; Bailey, 1955; Threinen, 1958; Colton, 1959; Alabaster, 1963; Clark, 1969), but the majority of work has involved laboratory determinations of thermal resistance.

An important question is: does a sublethal temperature shock disrupt subsequent thermoregulatory behavior of a fish? The objective of this study was to assess effects of temperature shock upon the thermoregulatory ability, selected temperatures, and locomotor activity patterns of individual bluegill, *Lepomis macrochirus*.

MATERIALS AND METHODS

Specimen

Juvenile bluegill (mean length 86.3 mm, range 72-105 mm) were captured during summer with electroshocking gear from Lake Wingra (Dane County, Wis.) and maintained in the laboratory at 25°C under constant photoperiod (LD 14:10 with 0.5 h dawn and dusk intervals) for at least 2 wk prior to experimentation. Throughout the preexperimental and experimental periods fish were fed pelleted food daily at 1630 h ± 15 min.

Apparatus

The thermoregulatory apparatus was derived from that of Neill and Magnuson (in press) with temperature control and rate-change modi-

[1]Laboratory of Limnology, Department of Zoology, University of Wisconsin, Madison, WI 53706.

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fications reported by Beitinger et al. (in press). The design (Neill, Magnuson, and Chipman, 1972) substitutes a temperature gradient over time for the spatial gradient typical of most temperature preference studies and allows an individual fish to serve as its own tank thermostat. Each 50-liter test tank was divided into halves with a molded fiber glass partition. A tunnel in the partition allowed the fish to choose between halves differing by a fixed 2°C temperature interval. When a fish selected the higher temperature, the temperature of the tank increased at a constant rate of 3°C/h while the 2°C differential between halves remained constant. When the fish moved to the cooler tank half, the temperature decreased at the same rate (3°C/h) until the fish again moved to the warmer tank half. By moving from one side to the other, a fish was able to control the temperature to which it was exposed. For this study, a potential temperature range of 4° to 55°C was available.

Temperatures of each tank half were monitored by a thermistor-wheatstone bridge circuit connected to a multichannel analog recorder. Avoidance temperatures (i.e., turnaround temperatures), preferred temperature range and midpoint of the preferred range (midpoint temperature) were the same as defined by Neill and Magnuson (in press). During the experiment, tunnel passes, recorded on an event recorder, were utilized as a measure of fish activity.

PROCEDURE

One fish was introduced per tank and allowed to experience the static system for 2.5 days with the tank halves set at 24° and 26°C. The test period then began and tank temperature control was relinquished to each fish. Thermoregulatory performance during the second, third, and fourth days constituted the pretreatment data. Then fish were removed and individually subjected to a sudden temperature change in 3.5-liter cylindrical chambers. The water in each chamber was well aerated and "conditioned" with 150 ml of that fish's thermoregulatory tank water. High temperature treatment was 36.1 ± 0.1°C and low temperature treatment was 21.0 ± 0.1°C. For control purposes, a third group of fish was treated at 31.0 ± 0.1C, a temperature approximating the preferred range midpoint for bluegill. A series of cursory experiments indicated that fish body temperatures equilibrated to the treatment temperature during exposure. Fish were randomly allocated to the three treatment temperatures. Following a 30-min exposure, each surviving fish was returned to its respective thermoregulatory tank for an additional 3-day posttreatment period. Thermoregulatory tank temperatures at fish reentry were the same as those at fish removal. Finally, fish were isolated and observed for 1 wk for possible latent effects.

RESULTS

Prior to treatment, there were no statistically significant differences in thermoregulatory performance among the three groups (Kruskal-Wallis one way analysis of variance; Siegel, 1956; lower and upper avoidance temperatures, midpoint temperature, and width of preferred range, all $P>0.20$). Fish had mean lower and upper avoidance temperatures of 29.3° and 33.1°C and mean preferred range width of 3.8°C. The

TABLE 1.—Lower and upper avoidance temperatures, preferred range midpoint and width, pretreatment and posttreatment, for each of the three groups. Means ± standard deviations are given.

Item	Controls 31.0°C	Cold shocked 21.0°C	Heat shocked 36.1°C	Grand mean
N	10	10	[1]12	
Lower avoidance temperature, °C:				
Pretreatment	29.4 ± 0.7	29.2 ± 0.9	29.4 ± 0.9	29.3
Posttreatment	29.4 ± 0.8	29.1 ± 1.0	30.0 ± 0.8	
Upper avoidance temperature, °C:				
Pretreatment	33.1 ± 0.6	33.1 ± 0.5	33.1 ± 0.9	33.1
Posttreatment	33.1 ± 0.7	33.1 ± 0.5	33.8 ± 0.9	
Midpoint of preferred range, °C:				
Pretreatment	31.3 ± 0.6	31.2 ± 0.6	31.2 ± 0.8	31.2
Posttreatment	31.2 ± 0.7	31.1 ± 0.7	31.9 ± 0.8	
Width of preferred range, °C:				
Pretreatment	3.7 ± 0.6	3.8 ± 0.7	3.7 ± 0.7	3.7
Posttreatment	3.6 ± 0.5	4.0 ± 0.8	3.8 ± 0.5	3.8

[1]One fish survived treatment but died during the first posttreatment night, owing to electronic failure.

midpoint of the preferred range was 31.2°C (Table 1).

Pretreatment and posttreatment comparison of preferred range midpoints for individual fish are illustrated in Figure 1. Of the 20 control and cold-treated fish (1b, a), 18 had posttreatment midpoint temperatures within 0.3°C of their pretreatment values. None of the individual control fish had significant pretreatment and posttreatment changes in mean avoidance temperatures (t-test, $P>0.05$). Among the cold-treated fish, two had significant downward changes in lower avoidance temperatures and one had a significant downward change in its upper avoidance temperature. In the control and cold-treated groups, five fish each had lower posttreatment midpoint temperatures; however, there were no significant trends (Wilcoxon matched pairs, signed ranks; controls and cold-treated $P>0.10$).

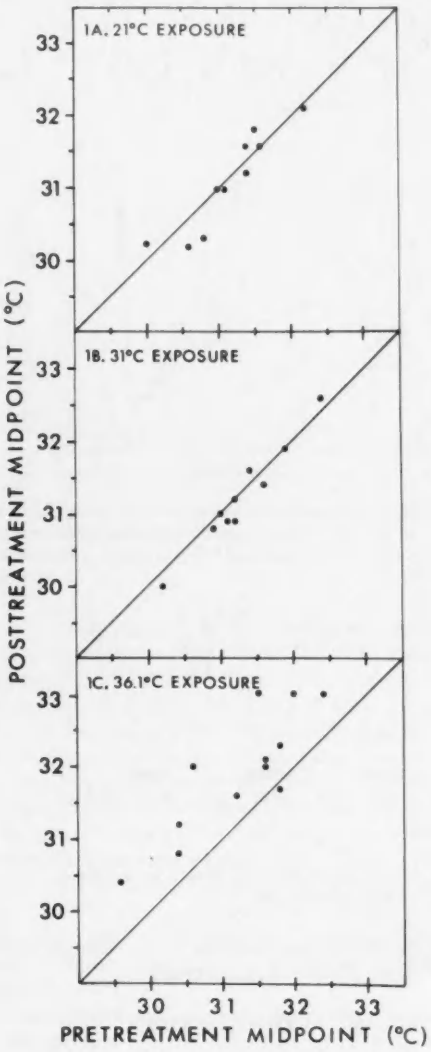

FIGURE 1.—Mean preshock and postshock midpoints of preferred range for individual bluegills in each of the treatment groups. Points falling on the 45° line indicate no change in midpoint temperatures.

Eleven of the twelve heat-treated fish had higher posttreatment midpoint temperatures (Figure 1c). This trend was highly significant (Wilcoxon matched pairs, signed ranks, $P<0.01$). The mean posttreatment midpoint temperatures for heat-treated fish during each of the 3 days were 31.9°, 32.0°, and 31.9°C, indicating no return towards the pretreatment preference level.

Whereas all of the control and cold-treated fish survived the treatment process, 7 of the 20 fish (35%) exposed to 36.1°C died during treatment. All fish that died lost equilibrium early in the treatment and were dead within 5 min. The mean pretreatment midpoint temperature of those that died was significantly lower than that of the survivors (Mann-Whitney U test $P<0.05$); however, temperatures experienced immediately prior to exposure were the same for both groups.

Although visual observations during the posttreatment period of this study were limited to avoid disturbing the fish, the typical immediate posttreatment behavior of both the heat- and cold-treated fish was submissive; often fish were hiding behind objects in their experimental tanks. However, at the feeding time, 4.5 h following exposure, nearly all fish actively fed.

A distinct diurnal pattern of activity was observed for each of the treatment groups throughout the 6-day experiment (Figure 2). Daytime hourly activities were typically two to three times higher than nighttime activities. The median activity (tunnel passes) of the cold- and, particularly, heat-treated fish dropped appreciably the hour following exposure (Figure 2). For general activity comparisons (Figure 3a, b) diurnal and nocturnal periods were separately analyzed (dawn and dusk excluded). With the pretreatment activity of each group serving as its own control, a series of Mann-Whitney U tests, with ties correction and z transformation were performed

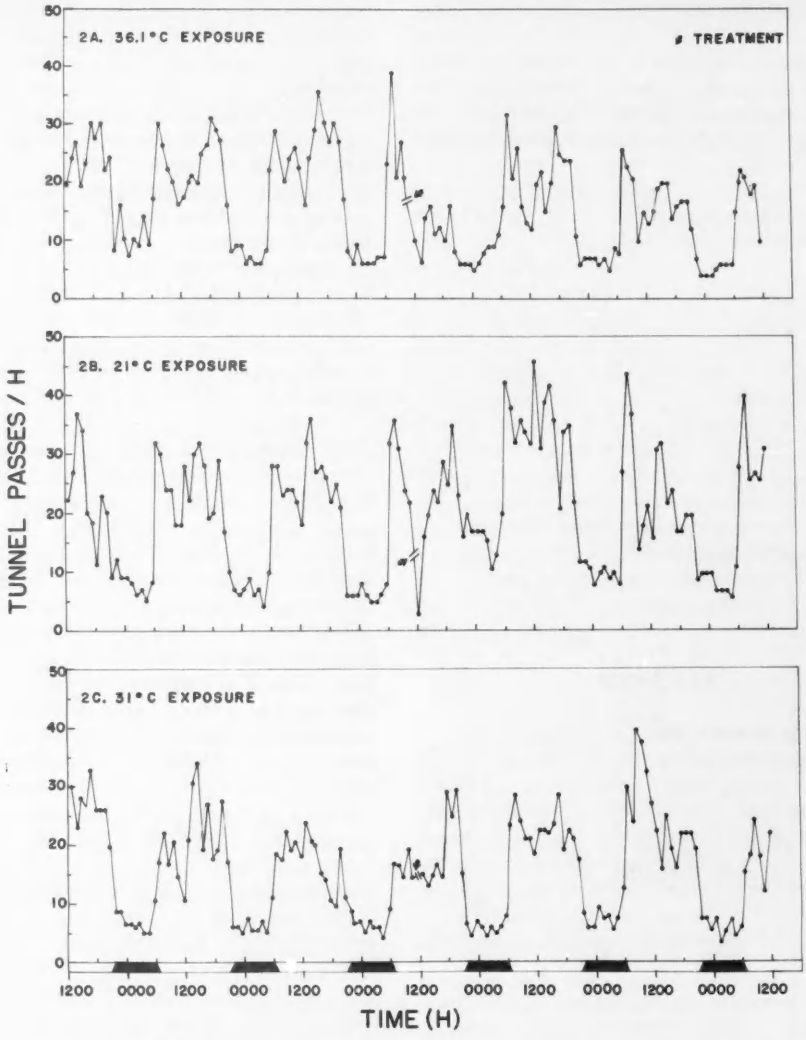

FIGURE 2.--Median hourly tunnel passes by fish throughout the entire 6-day experiment for each treatment group. The arrow indicates time of treatment.

to compare the 3-day pretreatment and 3-day posttreatment median hourly activities. The pretreatment and posttreatment activity levels of the control group were not significantly different. The daytime posttreatment activity of cold-treated fish, although higher and more variable, was not significantly changed; however, night activity increased ($P<0.001$). Heat-treated fish demonstrated the greatest change in activity. Both night and daytime activities decreased ($P<0.01$, $P<0.001$ respectively).

DISCUSSION

Combined pretreatment data demonstrate that the 32 test bluegills maintained their environmental temperatures within well-defined limits relative to the available temperature range. The

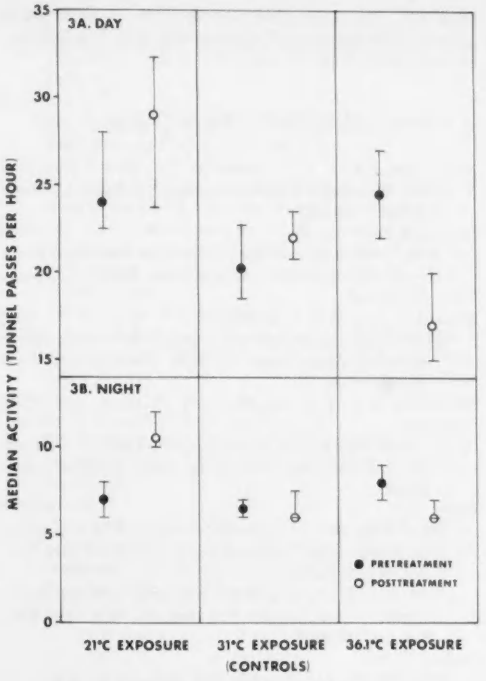

FIGURE 3.—Medians (circles) and 95% confidence limits for pretreatment and posttreatment bluegill hourly activities for the three treatment groups. Day and night activities are presented separately.

calculated midpoint of the preferred range, 31.2°C, is similar to that of Neill and Magnuson (in press), 30.4° and 0.8°C below the final temperature preferendum for bluegill reported by Fry and Pearson (1952).[2] The effect of sudden temperature stress on thermoregulatory behavior has not been previously examined. However, several other external factors have been reported to influence temperature preferenda, including season (Sullivan and Fisher, 1953; Zahn, 1963; Barans and Tubb, 1973), light intensity (Sullivan and Fisher, 1954), starvation (Javaid and Anderson, 1967) and exposure to chlorinated hydrocarbons (Ogilvie and Anderson, 1965; Peterson, 1973).

Pretreatment and posttreatment comparisons in the grouped control data clearly indicate no change in thermoregulatory performance. The Δt experienced by control fish was minimal and changes, if any, could be ascribed to handling or time-dependent variations in temperature preference.

Cold- and heat-treated fish actually experienced two temperature shocks. One occurred when the fish were introduced into the treatment chambers and the second when they were returned to their experimental tanks. Both cold and heat treatments were conducted at temperatures actively avoided by fish while in their thermoregulatory tanks.

Cold exposure did not significantly change any of the four measured parameters of thermoregulatory behavior. These fish experienced a Δt of approximately 10°C, but the exposure temperature, 21°C, is near the middle of the tolerance zone for bluegill. That these fish did not select lower temperatures was expected, owing to the slow rate of downward temperature acclimation characteristic of fishes (Brett, 1944, 1946). The lethal rates of temperature increase are at least 20 times the corresponding lethal rates of temperature decrease for bluegill (Speakman and Krenkel, 1971). Apparently, the 30-min exposure was not sufficient to change the acclimation state and, hence, the preferred temperature range of these fish.

Fish exposed to 36.1°C experienced a smaller Δt (about 5°C) during treatment, but this exposure was to within approximately 0.5°C of the bluegill's incipient upper lethal temperature (Hart, 1952; Cairns, 1956). The ability of surviving bluegills to thermoregulate was not deleteriously affected by the 30-min exposure to 36.1°C, however, statistically significant changes in avoidance and midpoint temperatures did occur. Thus, the thermoregulatory performance of bluegill was influenced more by exposure either to 1) temperatures closer to lethal limits than exposure to large Δt's per se or to 2) temperatures above rather than those below, the acclimation state of the fish.

Of the three exposure temperatures, only 36.1°C resulted in fish mortality. The pretreatment midpoint temperatures of these fish were significantly lower than those of fish surviving heat treatment, indicating a relationship between preferred and upper lethal temperatures. That a considerable proportion, 35%, of fishes exposed to 36.1°C died, is more important to the population than the observation that surviving

[2]Fry, F. E. J., and B. Pearson. 1952. Some temperature relations of the pumpkinseed and bluegill sunfish. Unpubl. manuscr., 10 p. Ont. Fish. Res. Lab. R.R. 2, Maple, Ont., Can.

fish had a 0.7°C increase in preferred range following exposure.

Use of tunnel passes as an index of locomotor activity is discussed by Beitinger et al. (in press). The diurnal activity pattern continued after treatment in all three groups (Figure 2). Immediately subsequent to treatment, a marked decrease in activity occurred in cold- and heat-treated fish but not in the control group (Figure 2). This decrease might help explain the increased susceptibility of thermally shocked fish to predation reported by Coutant (1972a, b, 1973) and Sylvester (1973). Hocutt (1973) found that exposure to rapid temperature changes, as large as 12°C below and 8°C above ambient temperatures, resulted in decreased swimming performance in juvenile largemouth bass, *Micropterus salmoides*; spotfin shiner, *Notropis spilopterus*; and channel catfish, *Ictalurus punctatus*.

Due to their mobility and acute temperature sensitivity, fishes are able to avoid environments of unfavorable temperatures. If trapped at these temperatures, fish possess the ability to resist thermal death. Ecologically, resistance ability affords a fish the opportunity to escape potentially lethal conditions at least until they lose equilibrium. Fish are exposed to stressful conditions when existing within their thermal resistance zone or when experiencing large temperature changes. The major objective of this research was to examine the thermoregulatory performance of bluegill following "high" and "low" thermal exposure. Nevertheless, the 35% mortality among 36.1°C treated fish and the severe depression in immediate posttreatment activity of both the 21.0° and 36.1°C treated fish were the two most ecologically important findings. All fish surviving treatment retained the ability to behaviorally thermoregulate, hence, disruption of thermoregulatory behavior is not a likely outcome of thermal shock in fishes.

ACKNOWLEDGMENTS

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DENSITY DISTRIBUTION OF JUVENILE ARCTIC COD, *BOREOGADUS SAIDA*, IN THE EASTERN CHUKCHI SEA IN THE FALL OF 1970

JAY C. QUAST[1]

ABSTRACT

The Arctic cod, *Boreogadus saida*, is a key element in the ecosystem of the Arctic Ocean. Juveniles, principally young-of-the-year, were taken by Isaacs-Kidd mid-water trawl at night during September and October 1970 in the eastern Chukchi Sea. Their average concentration was about 28/1,000 m^3 and their average biomass about 0.7 metric ton/km^2 of ocean surface. In 20 stations (representing about 30 x 10^3 km^2, or 8,714 square nautical miles), the number of juvenile cod (N) per standard haul (about 8,223 m^3 of water filtered per haul) increased with depth in meters (D) at about the same rate [$\log_{10}(N + 1) = 0.0669D$]. Yet the depth at which equivalent concentrations occurred varied over a range of 38 m between stations. The zone of increased concentration with depth, called a density structure, appears to be the nighttime relict of a graded negatively phototactic response to sunlight by the juvenile cod during preceding daylight. Apparently the structure was vertically displaced after dark by wind-induced upwelling and downwelling. The juvenile cod may have originated in the northwestern Bering Sea, off Arctic Siberia, or within the Chukchi Sea, and probably had recycled in the Chukchi Sea prior to capture.

This study of biomass and distribution of juvenile Arctic cod, *Boreogadus saida* (Lepechin), in the Chukchi Sea is an outgrowth of the Western Beaufort Sea Ecological Cruise of 1970 (WEBSEC-70) sponsored by the U.S. Coast Guard. My original objective was to explore the fishes of the marine ecosystem in the Arctic Ocean east of Point Barrow, Alaska, and if possible to quantify the occurrence of important forms. Because of an early southward shift of the arctic ice pack, the study was moved to the eastern Chukchi Sea. The sampling schedule—date, location, depth of water, and number and types of hauls—is given in Table 1 and Figure 1. The species of fish and where they occurred are summaried in Quast (1972).

Juvenile Arctic cod and Pacific sand lance, *Ammodytes hexapterus* Pallas, were virtually the only fish species trawled in the surface and mid-depths at night. The cod occurred at every station; also they were more numerous and had a larger biomass than the sand lance—a subjective estimate suggests a minimum 10 fold difference in both respects. Although sand lance were chiefly taken at the surface, the number of Arctic cod usually increased with depth. Because of the apparent importance of the Arctic cod in the off-bottom marine ecosystem of the eastern Chukchi Sea during WEBSEC-70, I further analyzed their data to estimate their numbers and biomass over the study area.

General life history, distribution, and literature on Arctic cod are summarized by Andriyashev (1954:195-198). The species is circumpolar and occurs to or nearly to the North Pole. Off Alaska, it occurs along the Arctic coast, in the Chukchi Sea, and in the Bering Strait; it also has been recorded in the winter from Norton Sound and the Gulf of Anadyr. Although most authors term the species "pelagic," "demersal" is probably better because adults appear to be associated with a shallowwater substrate, whether it be ocean bottom over the continental shelf or the undersurface of ice. Maximum size is about 320 mm total length (TL). Association with low temperatures is an important characteristic: Rass (1968: 136) gives the thermal environment of eggs as 0° to 2°C, of larvae as 2° to 5°C, and of fry as 5° to 7°C and probably higher. During WEBSEC-70, specimens of 0-age fish occurred at −1.5° to 3.5°C. According to Andriyashev (1954), Arctic cod mature when about 4 yr old and 190 mm TL; they spawn near coasts, principally in January

[1]Auke Bay Fisheries Laboratory, National Marine Fisheries Service, NOAA, Auke Bay, AK 99821.

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TABLE 1.—Station data for trawl collections in the eastern Chukchi Sea during WEBSEC-70.

Station	Date and inclusive time (Bering Standard)	Approximate position		Depth of water (m)	Hauls		
		Lat. N	Long. W		No.	Type[1]	Depths (m)[2]
10	27 Sept. (1917-2207)	70°04′	165°57′	44	4	R	11
14	29 Sept. (0518-0817)	70°17′	165°02′	51	4	R	11
16	29 Sept. (1721-2002)	70°16′	163°58′	53	4	R	11
20	30 Sept. (1740-2025)	70°20′	163°24′	42	4	R	12
22	1 Oct. (1734-2103)	70°20′	163°25′	35	4	R	12
25	2 Oct. (1731-2036)	70°07′	163°14′	33	4	R	12
30	4 Oct. (1756-2137)	69°58′	164°07′	31	5	M	2,5,10,13,19
32	5 Oct. (1831-2104)	69°48′	163°49′	26	4	R	12
37	6 Oct. (1727-1956)	70°07′	167°36′	49	4	R	12
41	7 Oct. (1752-2014)	69°57′	167°31′	44	4	M	10,10,12,22
45	8 Oct. (1816-2058)	69°57′	168°38′	44	4	M	2,9,13,20
51	9 Oct. (1744-2024)	69°36′	167°36′	48	4	M	2,7,14,20
56	10 Oct. (1940-2229)	69°14′	166°53′	44	4	M	2,9,18,23
61	11 Oct. (1755-2015)	69°05′	166°13′	29	4	M	8,13,16,23
65	12 Oct. (1755-2016)	69°21′	166°45′	36	4	M	8,13,16,22
70	13 Oct. (1735-1958)	69°12′	167°38′	39	4	M	8,13,18,22
74	14 Oct. (1723-1946)	69°35′	164°29′	22	4	M	2,8,13,18
80	15 Oct. (1814-2055)	69°27′	164°43′	30	4	M	2,8,13,22
88	16 Oct. (1917-2205)	68°55′	166°47′	45	4	M	2,11,24,40-45
92	17 Oct. (1733-2014)	68°36′	167°41′	54	4	M	2,13,17,33

[1]M = multidepth hauls with 1.8-m (6-foot) Isaacs-Kidd mid-water trawl, and R = replicate hauls at single depth.
[2]Depth at depressor.

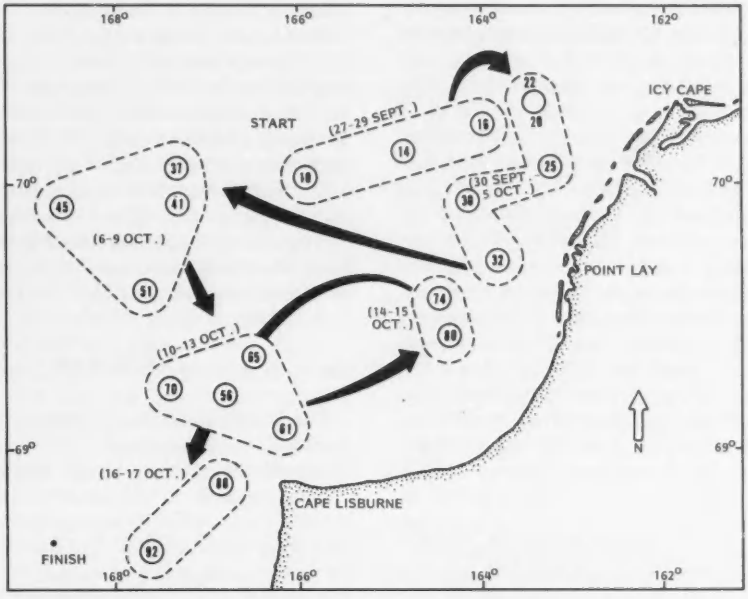

FIGURE 1.—Sequence and position of IKMT stations (circles) in the eastern Chukchi Sea in 1970. Dashed lines indicate time spans for groups of stations.

and February, and their eggs are large—approximately 1.5-1.9 mm in diameter. Rass (1968:136) adds that the first larvae appear in the sea in May-July; the larval stage (5.4-15.0 mm) lasts about 2 mo (in the Barents and Siberian Seas through June-July); and transition to juveniles is at 30-50 mm, in August.

Arctic cod appear to be a key species in the ecology of the arctic seas. They are widespread, locally abundant, and probably are a major element of the secondary consumer level in the trophic pyramid. Ponomarenko (1967:8) found that cod larvae and fry fed successively on copepod eggs, nauplii, and copepodites, and

Hognestad (1968:130) reported that adults trawled from the eastern Barents Sea in September 1966 fed principally on the copepod *Calanus finmarchicus*. In turn, Arctic cod are important as forage for higher level consumers. Andriyashev (1954:194-198) cites literature records for predation on Arctic cod by a long list of species, including char, saffron cod, flounders, sculpins, seals, walrus, beluga, sea gulls, alcids, and skuas. Tuck (1960:166) stresses the importance of Arctic cod in the diet of common and thick-billed murres of the polar basin, whose total populations contain at least 15 million birds (p. 51).

METHODS

Studies with the 1.8-m (6-foot) Isaacs-Kidd mid-water trawl (IKMT) involved 81 30-min tows (at depth) at 20 stations (Table 1). All stations were occupied for periods of about 2 h or more, and all but one started at late dusk or dark. The IKMT was similar in dimensions to the trawl tested and figured by Friedl (1971); it had a section of coarse mesh (3.8-cm bar) preceding 0.6-cm bar mesh. The cross-sectional area at the mouth was calculated as 2.87 m^2 and at the beginning of the 0.6-cm mesh as 1.55 m^2. To compensate for the possibility that fish would be herded into the small-mesh section by the coarse anterior mesh, a middle value between the two cross-sectional areas, 2.21 m^2, was arbitrarily used as the effective cross-sectional area of that portion of the net that captured juvenile cod. Calculation of the horizontal and vertical dimensions of the net swath was simplified by treating the effective cross-sectional area as a square—1.49 m on a side. Tows were standardized at 2 nautical miles (3,704 m) at depth by maintaining a vessel speed of 4 knots (estimated by engine revolutions) over 30 min. The resulting horizontal swath was calculated as 5,519 m^2 and the volume filtered as 8,223 m^3. At least four tows were made at each station, either at the same depth or at four different depths (Table 1)—two on one bearing and the remainder on its reciprocal.

Sampling followed a zigzag pattern (Figure 1) before a southward-advancing ice front. Because blocks of ice are sometimes difficult to see or become too abundant to avoid, mid-water trawling at night even in the presence of light pack ice is hazardous. The trawl can be seriously damaged or lost outright if a large block of ice becomes trapped beneath a trawl warp and causes the trawl to be lifted to the surface where the ice would be fed into its mouth at trawling speed. Consequently, trawling was usually done in the relatively open water of broad leads or ahead of the ice pack.

Two types of IKMT station were occupied. In one type (eight stations), nektonic organisms at a single depth within stations were sought by conducting four "replicate" hauls at 11 or 12 m (Table 1). In the other type (12 stations), the vertical distribution of nektonic organisms was sought by making four or five hauls at different depths (Table 1); the depths, which were usually verified with a bathykymograph, were selected after study of a Simrad[2] echogram (Model ER2—38 kHz). No reliable association was detected between presence or absence of bands on echograms and catch at those depths.

Data obtained on juvenile Arctic cod in the IKMT hauls included counts, range of standard lengths, and volumes. When large numbers of cod were captured, usually the total volume was measured and the number of cod was estimated from the average volume per individual in a subsample. When there appeared to be negligible differences in size of cod between hauls, the average volume per individual in one haul was used to estimate the number of juveniles in a volume taken in another haul at the same station.

RESULTS

The juvenile Arctic cod appeared to be principally of 0 age-class (young-of-the-year), based on a comparison between length frequencies of the Chukchi specimens and age-length data reported in the literature. For the comparison, the Chukchi data were converted from standard to total length by a regression based on data from the Chukchi Sea specimens (Table 2), because the measurement employed for data in the literature was not specific and therefore was assumed to be total length (the measurement usually used in fishery studies). Modal size of the Chukchi Sea specimens was 44 mm, slightly higher than the average size for age 0 cod, 35 mm, from the Barents Sea and Spitzbergen cited by Hognestad (1968:130). The

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Regressions of total length and volume on standard (body) length (X) in juvenile Arctic cod from eastern Chukchi Sea. Least squares fit to power equation, $Y = aX_b$, for 83 specimens over sizes 30<SL mm<74.

Measurement (Y)	a	b	Correlation coefficient
Total length (mm)	1.4429	0.9478	0.996
Volume (ml)	0.4454×10^{-4}	3.1678	0.984

upper limits of nearly all size distributions by haul from the Chukchi Sea, 35 of 40, were below the mean size for age I cod cited by Hognestad. Because the cod from the Chukchi Sea were captured in September and October, at a later date than Hognestad's specimens, there is little doubt that most specimens captured in the eastern Chukchi Sea were age 0.

Homogeneity of sampling variance was then examined in the data on frequency of occurrence of juvenile cod in the hauls by comparing within-station (single depth) standard deviations from the replicate stations. Three hauls also were included from one multidepth station because they were taken at about the same depth, 11 m, as the hauls at the replicate stations. Standard deviation appeared to be proportional to the mean in the comparisons (Table 3), strong evidence that the sampling variance was not homogeneous. The variance appeared to be stabilized by logarithmic transformation of the frequencies [$\log_{10}(N + 1)$] which then passed Bartlett's test (Table 3). As a result, the logarithmic transformation was applied to the analysis of frequencies.

The frequency data were examined by analysis of variance to determine the significance of between-station differences in population density. Data from multidepth stations were not used because these stations were not standardized for depth. Significant between-station differences were present (Table 4), evidence that there were important horizontal differences in density of Arctic cod over the sampling area, at least at depths of 11-12 m.

TABLE 4.—Analysis of variance of numbers (transformed) of juvenile Arctic cod in IKMT hauls at eight replicate stations in eastern Chukchi Sea.

Source	d.f.	S.S.	M.S.	F
Among stations	7	10.60984	1.51569	8.84; $P<0.001$
Within stations	24	4.11693	0.17154	—
Total	31	14.72677	—	—

Capture rate of juvenile cod consistently increased with depth and the slope of regressions of number of captures on depth was similar among the multidepth stations. Also, regressions at the stations appeared to bear no direct relationship to salinity structure nearby (Figure 2). Significance of differences between the regressions was tested by analysis of covariance with the result that differences in slope were judged as insignificant. Differences in level, however, did appear to be significant (Table 5). Apparently concentration of juvenile Arctic cod increased at about the same logarithmic rate (0.0669) with depth, but the depth at which a given concentration occurred varied between stations. This triangular area on the plots (Figure 2), with its apex toward the surface, was regarded as the graphic analog of the relationship between concentration and depth in the juvenile cod; it was termed a "density structure." Evidently the density structure was relatively stable relative to the time span of sampling at a station (about 2 h) because the structure was always evident despite the depth sequence of hauls (Figure 2).

TABLE 3.—Comparison of means, standard deviations, and variances for raw and transformed frequencies of occurrence [$\log_{10}(N + 1)$] of juvenile Arctic cod between replicate stations in eastern Chukchi Sea. Data arranged in order of increasing means in the transformed data.

Station	No. replicate hauls	Raw data Mean	Raw data SD	Raw data Variance	Transformed data Mean	Transformed data SD	Transformed data Variance[1]
37	4	3.3	4.0373	16.3	0.4758	0.4273	0.1826
32	4	6.3	5.4406	29.6	0.7751	0.3079	0.0948
14	4	20.8	22.0681	487.6	1.0397	0.7333	0.5377
25	4	23.3	31.9312	1,019.6	1.1380	0.5011	0.2511
20	4	51.8	47.7169	2,276.9	1.6159	0.3260	0.1063
22	4	57.0	56.3090	3,170.7	1.6399	0.3516	0.1236
16	4	62.5	28.2436	797.7	1.7612	0.2347	0.0551
41	[2]3	277.7	202.5075	41,009.3	2.3101	0.4795	0.2299
10	4	258.0	87.2221	7,607.7	2.3954	0.1453	0.0211

[1]Bartlett's Test for Homogeneity (Sokal and Rohlf, 1969:370, 371): $\chi^2 = 4.004$, $P>0.5$.
[2]A multidepth station in which three hauls were at approximately 11 m.

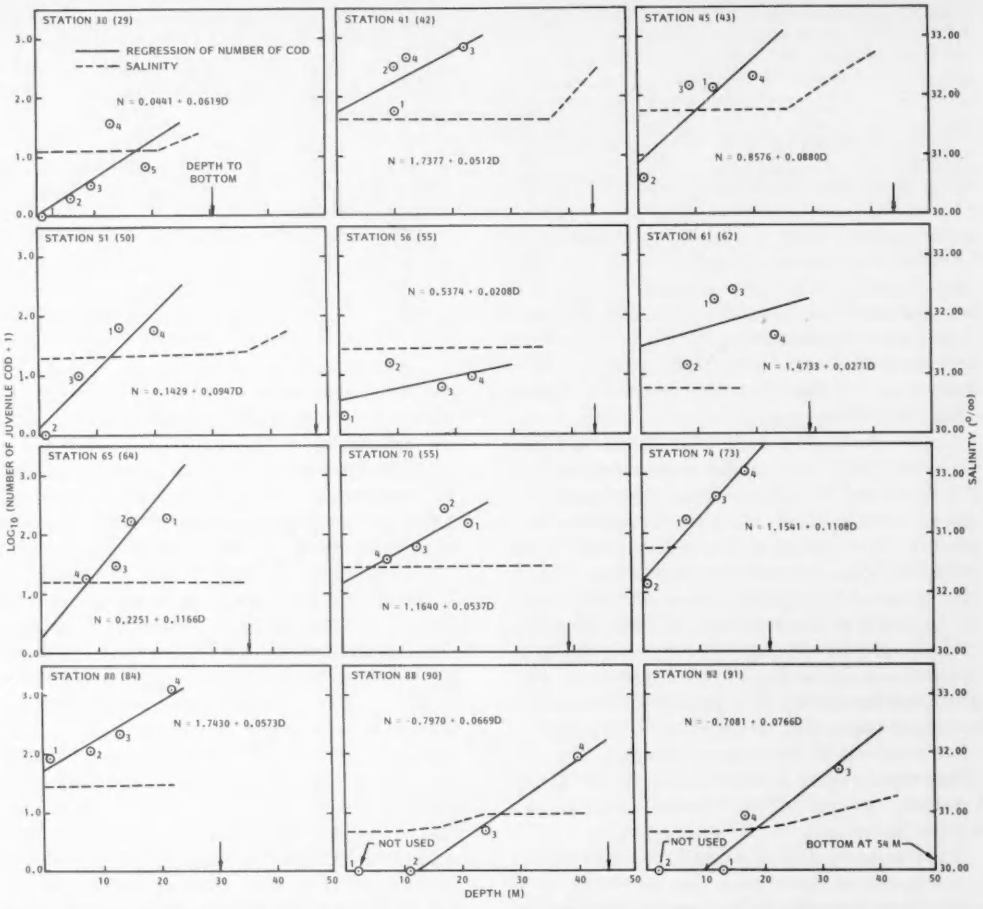

FIGURE 2.—Depth distribution of juvenile Arctic cod and salinity at the 12 multidepth stations. Salinities from the nearest oceanographic station (number in parentheses) from Ingham and Rutland (1972) and U.S. National Oceanographic Data Center. Numbers on points indicate sequence of hauls. Regressions of number of cod (N) on depth in meters (D) fitted by least squares. Pooled slopes for all data = 0.0669.

TABLE 5.—Analysis of covariance on data for abundance and depth of juvenile Arctic cod at 12 multidepth stations in eastern Chukchi Sea.

Source	*d.f.*	*S.S.*	*M.S.*	*F*
1. Individual regressions	23	3.91335	0.17015	—
2. Difference between 1 and 3 for testing slopes	11	1.48432	0.13494	(2)/(1) = 0.79; n.s.
3. Individual regressions fitted with a common slope	34	5.39767	0.15876	—
4. Difference between 3 and 5 for testing levels	11	23.56263	2.14206	(4)/(3) = 13.49; $P<0.005$
5. Regressions fitted to a single line	45	28.96030	—	—

DISCUSSION

Possible Causes of the Density Structure and Its Vertical Displacement

The steady increase of number of cod in the density structure with depth indicated a graded rather than a threshold response to some environmental factor, because if the response depended on a threshold, one would expect a sudden increase in density of juvenile cod when that threshold was reached. Salinity relationships in the water column did not appear to be a cause of the density structure because the water column was usually nearly isohaline through the region of greatest change in concentration of juvenile cod (Figure 2)—the density structure evidently persisted despite forces that contributed to oceanic mixing. Predation by aquatic predators did not seem to be a reasonable cause because the only evident potentially effective fish or invertebrate predator on the cod was large jellyfish, which occurred in approximately equal numbers throughout the water column. Reaction of the juvenile cod to a pressure gradient also was dismissed, for reasons discussed below.

A graded negative phototaxis either in the juvenile cod or, possibly, in the prey they were following seemed to offer the best hypothesis for the cause of the density structure and its variations. A gradient of increasing darkness with depth could coincide closely with the gradient for increase in number of cod. This type of gradient is illustrated in Figure 3 (shown here for the English Channel—the slope in regard to perception by the cod should be dependent on turbidity as well as the spectral sensitivity of the juvenile cod). Under this hypothesis the density structure of juvenile cod found at night was a relict of earlier daylight hours, during which the density structure was maintained despite turbulence, upwelling, and downwelling. With onset of darkness the means of orientation by the fish was removed and the density structure was elevated or depressed, depending on whether it occurred in cells of upwelled or downwelled water. The density structure presumably persisted into the early night when most hauls were made because of the short period of time elapsing before trawling began and also because the cod were relatively inactive at the low sea temperatures

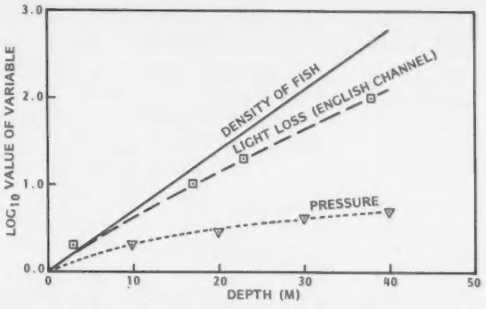

FIGURE 3.—Conformity of the variables—density of juvenile Arctic cod, loss of light (blue-green, English Channel), and pressure at increasing depths. Regression of fish with depth (D), $\hat{N} = 0.0699D$, where $\hat{N}$ = most likely number of fish in a trawl swath (see text); index of light loss based on $I = \log_{10}(1/p \times 100)$, where p = percent of illumination at surface, from data of Nicol (1960:22); and pressure (atmosphere) based on an increase of 1 atm/10-m depth, after Nicol (1960:22).

(−1.5° to 3.5°C). The freshly trawled specimens were markedly inactive. The validity of the gradient hypothesis possibly could have been evaluated further had trawl data been available for daylight hours. Data on vertical distribution of zooplankton were not available because sampling was entirely by vertical tows (Wing, in press).

Orientation by the cod to a pressure gradient was dismissed as an explanation of the density structure for two reasons: the shape of the curve of pressure on depth differs from that of the density structure (Figure 3), and orientation to a pressure gradient should be the same during the day as at night and should not allow the density structure to be elevated or depressed.

If the density structure were a result of behavior in the juvenile cod, it may have been evolved in response to predation by birds. Undoubtedly, such predation is a factor of tremendous ecological importance to juvenile cod, primarily during summer when bird populations are at their peak. Arctic piscivorous birds form a spectrum of depth capabilities, and because their feeding is based at the surface, intensity of predation should decline with depth, i.e., complement the density structure. Watson and Divoky (1972) give an extensive list of bird species observed in the Chukchi Sea during WEBSEC-70, the majority of which are either recorded as predators or are assumed to have, and to make use of, the potential for predation on juvenile Arctic cod. Included are loons, slender-billed shearwater, pelagic

cormorant, red phalarope, glaucous gull, herring gull, ivory gull, black-legged kittiwake, Ross's gull, Sabine's gull, murres, guillemot, Kittlitz's murrelet, parakeet auklet, and horned puffin. Swartz (1966:674) estimated a population of about 600,000 piscivorous birds (adults and fledglings) at Cape Thompson, which is south of Cape Lisburne, in 1960; murres and kittiwake gulls accounted for 90% of the population. He estimated that the birds consumed approximately 13.5×10^3 metric tons of food during their breeding season. Tuck (1960:166) found that Arctic cod were the most important fish in the diet of murres, as did Swartz (1966:667) in his studies at Cape Thompson. Tuck cited depth records for murres which indicate that they are able to feed throughout the entire water column over the shelf portion of the Chukchi Sea. Since the birds at Cape Thompson are undoubtedly only a small fraction of the birds that utilize the southern Chukchi Sea, predation on fishes by birds must be intense over the entire region. However, bird predation could not have been a direct cause of the density structure during WEBSEC-70 because most birds appeared to have left the region prior to the time of our visit.

The hypothesis of negative phototaxis in juvenile Arctic cod had further appeal—it seems congruent to presumed needs for lowering vulnerability to predation by birds during summer when subsurface illumination is high while allowing for vertical foraging by the cod when illumination is low. Because piscivorous birds undoubtedly are visual feeders, directed or passive movement toward the surface by juvenile cod at night should not be counterselective. During the prolonged periods of low illumination of arctic winter, and under ice cover, juveniles presumably would be able to occupy the entire water column over the continental shelf. However, because larger juveniles, about 15 cm TL, were commonly seen in daylight near ice that had been broken by the icebreaker, negative phototaxis of the juveniles, if present, must decrease with growth in favor of life near a substrate. Changes from a pelagic to demersal existence during early growth stages is a commonplace in fishes.

Upwelling and downwelling seemed a plausible explanation of the differences in depth noted for the density structure. Salinity of the upper water column and an index of elevation or submergence of the density structure, explained below, showed good correlation (Table 6). The index was obtained for each station by algebraically projecting the pooled value for slopes of all regressions of number vs. depth, multidepth and replicate stations, through the station data, to the hypothetical apex of the density structure at the station. If the apex lay above the ocean surface (e.g., Figure 2, stations 41 and 70), the converted amount in meters was negative and was taken as the amount the density structure was elevated. If the apex lay below the ocean surface (e.g., Figure 2, stations 88 and 92), the converted amount in meters was positive and was taken as the amount the density structure was submerged. For each replicate station the regression was based on a point determined by depth of trawling and the average number of juvenile cod captured at the station. All indices for salinity were based on data for 10-18 m because this zone was the common depth of the replicate hauls; however, the water column was usually nearly isohaline from the surface to considerably below this depth (Figure 2).

Two sources of upwelling seemed possible—an accelerated current around the Cape Lisburne-Point Hope headland and wind over the sampling

TABLE 6.—Comparison of hypothetical elevation of the density structure of juvenile Arctic cod at the trawl stations taken at late dusk or after dark, based on density distribution of cod at each station, with surface salinity at a nearby station. Stations in order from greatest submergence (positive values) to greatest elevation (negative values) of the density structure. Projections for the multidepth stations were based on the data of Figure 2 fit to the standard slope of 0.0669; methods for obtaining projections from the replicate data are explained in the text.

IKMT station and type [1]	Indicated level of apex in meters	Closest oceanographic station	Average salinity at 10-18 m
88(M)	11.9	90	30.72
92(M)	10.5	91	30.67
37(R)	4.9	36	31.65
32(R)	0.5	31	30.85
30(M)	-0.7	29	31.11
51(M)	-2.1	50	31.32
65(M)	-3.4	64	31.19
25(R)	-5.0	24	31.00
56(M)	-8.0	55	31.43
20(R)	-12.2	19	31.72
22(R)	-12.5	19	31.72
45(M)	-12.8	43	31.76
16(R)	-15.3	18	31.11
74(M)	-17.3	73	31.77
70(M)	-17.4	55	31.43
61(M)	-22.0	62	30.76
10(R)	-24.8	9	31.56
41(M)	-26.0	42	31.63
80(M)	-26.1	84	31.47

$r = -0.514$; $P<0.05$

[1] M = multidepth station; R = replicate station.

area. Both should produce transient cells of upwelling and downwelling, but the wind-caused cells should have broader distribution.

Currents apparently flow predominantly northward in the southern Chukchi Sea and accelerate around headlands (Fleming and Heggarty, 1966: 744). Therefore, at an early stage in analysis, it appeared that the density structure of juvenile cod encountered during WEBSEC-70 may have been a result of bird predation off the Cape Lisburne-Point Hope headland or in Kotzebue Sound with subsequent vertical displacement of the density structure in an eddy north of Cape Lisburne. However, this hypothesis was rejected because, as mentioned previously, birds were not abundant during WEBSEC-70; most of them had probably left the region at least a month previously. Moreover, oceanic mixing should quickly dissipate a density structure that formed near the cape. The apparent occurrence of the structure over the entire sampling area indicated that it 1) was quite permanent, 2) was probably maintained by the juvenile cod, and 3) was not in very large measure induced by currents around Cape Lisburne. These requirements were satisfied by the hypothesis of negative phototaxis and wind-induced upwelling.

Horizontal Density Distribution of Juvenile Cod

Regardless of possible origins of the density structure or reasons for its vertical displacement, it was necessary to take the vertical elevation of the density structure (Table 7) into consideration when estimating the concentration and biomass of juvenile cod at each station. This correction was accomplished by regarding the density structure as a unit that extended downward 47 m (the depth equivalent on the density structure of the highest number of cod sampled) in undisturbed water. The structure would be truncated in its upper part by the ocean surface when raised, or truncated in its lower part when it intersected the ocean bottom because of lowering of the structure or shallowness of the sea. Thus, for a structure that appeared to be raised 10 m in the water column, the number of cod remaining in the structure was taken as the number that occurred between 10 and 47 m in an entire structure. If a structure appeared to be truncated by the ocean bottom for 17 m, the number of cod remaining in the structure was taken as the number between 0 and 30 m in an entire structure. Estimation of the density of

TABLE 7.—Reconstruction of numbers of juvenile cod beneath a standard swath at the IKMT stations, eastern Chukchi Sea.

Station (type)	Depth of tows (m)	Average $\log_{10}(N+1)$	Indicated level of apex in meters[1]	Density structure		Depth of water (m)	No. cod below density structure	Total for column beneath swath
				Depth of base (m)	Juvenile cod (no.)			
10(R)	11	2.3954	-24.8	22.2	4,698	44	7,883	12,581
14(R)	11	1.0397	-4.5	42.5	5,184	51	3,222	8,406
16(R)	11	1.7612	-15.3	31.7	5,138	53	8,073	13,211
20(R)	12	1.6159	-12.2	34.8	5,179	42	2,729	7,908
22(R)	12	1.6399	-12.5	34.5	5,176	35	[2]	5,366
25(R)	12	1.1380	-5.0	42.0	2,462	33	[2]	2,462
30(M)	—	regression	-0.7	46.3	1,268	31	[2]	1,268
32(R)	12	0.7751	0.5	47.5	547	26	[2]	547
37(R)	12	0.4758	4.9	51.9	4,162	49	[2]	4,162
41(M)	—	regression	-26.0	21.0	4,595	44	8,717	13,312
45(M)	—	regression	-12.8	34.2	5,173	44	3,714	8,887
51(M)	—	regression	-2.1	44.9	5,181	48	1,175	6,356
56(M)	—	regression	-8.0	39.0	[3]5,190	44	1,895	7,085
61(M)	—	regression	-22.0	25.0	4,891	29	1,516	6,407
65(M)	—	regression	-3.4	43.6	2,798	36	[2]	2,798
70(M)	—	regression	-17.4	29.6	5,088	39	3,563	8,651
74(M)	—	regression	-17.3	29.7	2,681	22	[2]	2,681
80(M)	—	regression	-26.1	20.9	4,586	30	3,449	8,035
88(M)	—	regression	11.9	58.9	1,492	45	[2]	1,492
92(M)	—	regression	10.5	57.5	3,968	54	[2]	3,968

[1]Negative values indicate apex above the surface.
[2]Stations at which hypothetical depth of bottom of density structure is deeper than the bottom. The number of juvenile cod represented by the overlap is subtracted from the total.
[3]In some instances the number of juvenile cod estimated for a density structure that was truncated at the surface was slightly higher than the theoretical number in an entire density structure. This discrepancy seems to be due to rounding errors in the integrations about the point where the parabolic equation approaches and forms a small angle with the x-axis. Since very few juvenile cod were present in the apex of the density structure, the error is small and probably unimportant.

juvenile cod below the presumed density structure was a problem because data from near bottom were not available for many stations. Therefore, the density of juvenile cod below the structure was assumed to be the maximum calculated for the density structure (i.e., that at 47 m in an entire structure). The possible error in estimating biomass of juvenile Arctic cod at the stations under this assumption was not judged to be serious because the sampling area was so shallow that the bottom of the density structure was usually close to the ocean bottom.

Although the transformed data on cod abundance vs. depth were useful for analyzing the density structure at the stations, back transformation of the estimates offered problems of interpretation. At present there appears to be no practical procedure for back transforming the variance and estimates of a logarithmic-arithmetic regression. Consequently, the density structure was redescribed from the untransformed data by fitting a parabolic regression with least squares (Figure 4). The variables were weighted by the inverse of the corrected depth squared because the variance of number of cod vs. depth appeared to be linearly related to the square of the corrected depth. The result was

$$Y = 6.72605 - 3.63466X + 0.33017X^2$$

and its integration

$$Y^* = \int_U^L Y\ (X)\, dX$$

$$= 4.51413\ (L - U) - 1.21968\ (L^2 - U^2) + 0.07386\ (L^3 - U^3)$$

where Y = most likely estimate of number of cod in a tow at corrected depth.
X = corrected depth in meters.
Y^* = most likely estimate of the number of cod over the depth interval U-L in a trawl swath.
U = upper (shallower) level of depth interval, where $0 \leq U \leq L \leq 47$.
L = lower (deeper) level of depth interval.

Accordingly, the density structure contained approximately 5,186 juvenile cod over its depth range (0-47 m) over the area of a trawl swath. The most likely estimate of maximum density, at 47 m, was 379 cod/m of depth over the area of a trawl swath (5,519 m²).

Under these assumptions, composite estimates of the number of juvenile Arctic cod in the water column beneath a standard trawl swath was calculated for all IKMT stations (Table 7). Totals for each station were obtained by adding the number of juvenile cod estimated for that section of the water column occupied by the density structure—5,186 over 47 m of depth except when the structure was truncated by the surface or bottom—to the hypothetical number in the column below the structure, or 379/m of depth. For the replicate stations, where only one depth was sampled, the hypothetical depth of the structure was obtained by comparing the average catch (log transformed data) at the trawling depth with the catch (log transformed data) that would be expected at that depth if the apex of the density structure coincided with the ocean surface. If this comparison indicated that the apex of the hypothetical structure was projected above

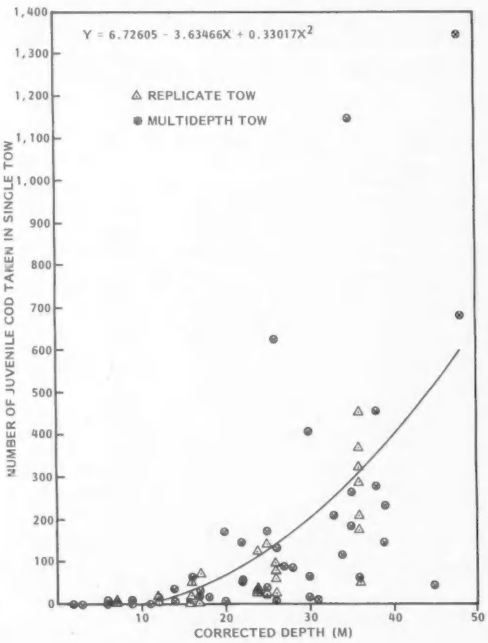

FIGURE 4.—Number of juvenile Arctic cod per Isaacs-Kidd tow, the depths corrected for apparent emergence or submergence of the density structure (Tables 6 and 7). Weighted regression ($1/X^2$) fitted by least squares.

the ocean surface (indicated by minus values for level of apex in Tables 6 and 7) or below the ocean bottom, then the appropriate adjustments, discussed previously, were made. As a result, estimates of juvenile cod at the IKMT stations were influenced by both an inferred height of the density structure and the depth of water beneath the structure. Stations in relatively shallow water and with a deeply submerged density structure had the lowest estimates, and stations in water deeper than average and with density structures that reached to the surface had the highest. The average for all stations was 28.5 juvenile cod/1,000 m³ (Table 8).[3]

Biomass of juvenile Arctic cod in the area surveyed by WEBSEC-70 was estimated by converting the overall average concentration to volume and weight. Average volume of individuals in samples was 0.618 ml, with no apparent size segregation with depth (Figure 5). If we assume that the specific gravity of the cod approximated unity (actually they were heavier), then the stations averaged 17.6 g of juvenile cod/1,000 m³. If we take the area surveyed in the eastern Chukchi Sea as approximately 30 x 10^3 km² (8,714 square nautical miles) and the average depth as 40.0 m (the average for the 20 IKMT stations), then approximately 12 x 10^{11} m³ of ocean were contained in the sampling area. Thus, it appears that 211.2 × 10^8 g of fish were represented by this volume, or 211.2 × 10^2 metric tons, for an average of 0.7 metric ton/km² of ocean surface.

Where did the juvenile cod originate? Likely sources appear to be the Bering Sea, the East Siberian Sea, or the Chukchi Sea itself. The northwestern part of the Bering Sea has particularly low temperatures (Zenkevitch, 1963:824, 825) and water from the Gulf of Anadyr tends to flow northeastward (Zenkevitch, 1963:821). The East Siberian Sea, of course, also has low temperatures and apparently has an eastward-flowing current

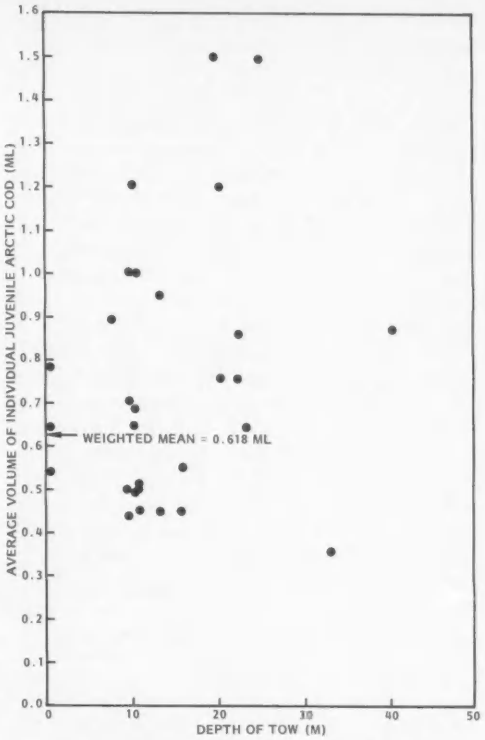

FIGURE 5.—Relation of average volume (milliliters) of individual juvenile Arctic cod in IKMT tow to depth of capture, eastern Chukchi Sea.

[3]This compares with an arithmetic average of 7.3/1,000 m³ for the replicate hauls and 19.5 for the multidepth hauls—an average of 13.4 for all hauls. Thus, simple arithmetic averaging would seriously underestimate the value obtained under the hypothesis of density structure with upwelling and downwelling. Even higher values would be obtained if it is assumed that the density structure continued to increase at the same logarithmic rate below its depth of 47 m until the bottom was reached, instead of having the increase truncated at 47 m. This approach would require extrapolation well beyond all observed values for fish densities and would not be fully consistent with the welling part of the hypothesis.

TABLE 8.—Estimated volume of water and number of juvenile cod beneath a standard swath at the IKMT stations, eastern Chukchi Sea.

Station	Volume of water beneath trawl swath (m³)	Juvenile cod/1,000 m³
10	242,836	51.8
14	281,469	29.9
16	292,507	45.2
20	231,798	34.1
22	193,165	27.8
25	182,127	13.5
30	171,089	7.4
32	143,494	3.8
37	270,431	15.4
41	242,836	54.8
45	242,836	36.6
51	264,912	24.0
56	242,836	29.2
61	160,051	40.0
65	198,684	14.1
70	215,241	40.2
74	121,418	22.1
80	165,570	48.5
88	248,355	6.0
92	298,026	13.3
Weighted average	—	28.5

into the Chukchi Sea (Zenkevitch, 1963:262). The near absence of high-arctic zooplankton in the eastern Chukchi Sea (Zenkevitch, 1963:268), verified during WEBSEC-70 by Wing (in press), is only weak evidence that the cod did not originate in the East Siberian Sea: the cod probably spawned in January and February (Rass, 1968:136), approximately 8 mo before WEBSEC-70, and it seems possible that the juveniles could have lost their arctic ecological associates over that period of time. In any event, the apparent short time that cod spent in some sections of the Chukchi Sea—about 10 days in the southeastern part according to the oceanographic data of Fleming and Heggarty (1966: 724)—and the time elapsed between spawning and capture at our IKMT stations is evidence that the juvenile cod either originated at considerable distances from the Chukchi Sea or had been cycled in the Chukchi Sea. Since there is reason to believe that a portion of the Chukchi Sea circulates in a counterclockwise gyre (Zenkevitch, 1963:262), similar cycling of eggs and larvae seems possible.

SUMMARY

1. Twenty stations in the eastern Chukchi Sea between Icy Cape and Cape Lisburne were sampled with a 1.8-m (6-foot) Isaacs-Kidd mid-water trawl (IKMT) during September and October 1970.

2. Only two species of fish occurred in any abundance in the middle and upper water column at night, juvenile Pacific sand lance and juvenile Arctic cod (mostly age 0). Because the Arctic cod were most abundant and were distributed through most of the water column, their occurrence was given a detailed analysis.

3. Two types of IKMT stations were occupied; one in which hauls were replicated at the same depth, and another in which hauls were made at several depths. All stations but one (a replicate station) were occupied starting at late dusk or at night.

4. The standard deviation in frequency of juvenile cod occurrence at the replicate stations seemed to be proportional to the means. The variance was stabilized by $\log_{10}(N + 1)$ transformation of the data.

5. Analysis of variance of the transformed data from the replicate stations disclosed significant between-station variation in number of cod occurring at 11-12 m.

6. Number of juvenile cod per unit volume of water increased with depth at all multidepth stations.

7. Analysis of covariance on regressions of cod abundance ($\log_{10}$ transformed) vs. depth disclosed no significant differences in slope of the regressions between stations but significant differences in level.

8. The characteristics of slope and level in the regressions for multidepth stations described a depth region of logarithmic increase in concentrations of juvenile cod. This region was at a different depth at some stations than at others and was called a density structure.

9. It appeared that the density structure resulted from a graded rather than a threshold response to subsurface illumination. Such a response seems to be a suitable behavioral strategy for lessening predation by piscivorous birds.

10. The hypothesis is presented that the density structure was formed during daylight hours and that differences in its vertical displacement between stations at night were caused by wind-induced upwelling or downwelling.

11. Average number of juvenile cod calculated for the stations was 28/1,000 m^3 or approximately 0.7 metric ton/km^2 of ocean surface.

12. The origin of juvenile cod could have been in the northeastern Bering Sea, the East Siberian Sea, the Chukchi Sea, or all three. Regardless of origin, a cycling of eggs and larvae within the Chukchi Sea seems likely.

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DESCRIPTION OF EGGS AND LARVAE OF SCALED SARDINE, *HARENGULA JAGUANA*[1, 2]

EDWARD D. HOUDE,[3] WILLIAM J. RICHARDS,[4] AND VISHNU P. SAKSENA[5]

ABSTRACT

Eggs and larvae of scaled sardine, *Harengula jaguana*, were described from specimens reared in the laboratory. Meristics, morphometrics, osteology, and pigmentation were examined as development proceeded. Transformation of larvae to the juvenile stage was complete at 22 to 24 mm standard length. During transformation outstanding features included forward movement of the dorsal fin, shortening of the gut, and forward movement of the anal fin. Eggs and larvae of scaled sardine were compared with those of other clupeids that may occur in the same areas. An illustrated series of scaled sardine eggs and larvae, including details of the caudal fin, was presented to show changes that occur during development.

Scaled sardines, *Harengula jaguana* Poey, are common clupeids in the tropical western Atlantic (Rivas, 1963). Until recently they were known as *H. pensacolae* Goode and Bean, 1879, but Whitehead (1973) has concluded that the correct name for the species is *Harengula jaguana* Poey, 1865. Scaled sardines prefer coastal habitats and have been reported from New Jersey to Brazil; they are abundant in the Gulf of Mexico (Briggs, 1958; Rivas, 1963; Berry, 1964b). Despite their common occurrence, larvae have not been described. Matsuura (1972) has described artificially fertilized and planktonic eggs of this species. Fecundity, maturation, and spawning of scaled sardines recently were reported by Martinez (1972). Eggs have been collected in south Florida, and the larvae reared to juvenile sizes in the laboratory (Houde and Palko, 1970; Detwyler and Houde, 1970; Saksena and Houde, 1972). Eggs and larvae from these experiments have provided us with material to describe early development.

Scaled sardines support a small bait fishery in south Florida and are important forage for predatory fishes like Spanish mackerel, *Scomberomorus maculatus* (Klima, 1959). They are caught for human consumption throughout the West Indies and are canned in Cuba and Venezuela (Rivas, 1963). Scaled sardines are one of the clupeid species that may have potential to support reduction fisheries in the tropical Atlantic.

Eggs and larvae of other species attributed to the genus *Harengula* have been described. Uchida et al. (1958) described larvae and juveniles of *H. zunasi* from Japan, and Takita (1966) described eggs and newly hatched larvae of that species. Whitehead, Boeseman, and Wheeler (1966) stated that this species is in fact a *Sardinella*, based on skeletal characters. Marchal (1967) included *H. rouxi* in his key to some west African clupeid eggs and larvae. Berry (1964a) and Berry and Whitehead (1968) restricted the genus *Harengula* to members having paired hypomaxillary bones. Neither *H. rouxi* nor *H. zunasi* have hypomaxillaries, and both species presumably belong in the genus *Sardinella*.

METHODS

Eggs were collected in surface tows of plankton nets near Miami Beach and in Biscayne Bay, Fla. during 1969 through 1971. A total of 10 embryos and 165 larvae from rearing experiments were preserved in 5% Formalin[6] to describe

[1]Contribution No. 1786, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149.
[2]Contribution No. 235, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, FL 33149.
[3]Rosenstiel School of Marine and Atmospheric Science, University of Miami, Division of Fisheries and Applied Estuarine Ecology, 10 Rickenbacker Causeway, Miami, FL 33149.
[4]Southeast Fisheries Center, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149.
[5]Department of Biology, Muskingum College, New Concord, OH 43762.

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[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

development. Rearing methods have been described (Houde and Palko, 1970; Saksena and Houde, 1972). Scaled sardines can be reared successfully at temperatures from 21° to 33.5°C (Saksena, Steinmetz, and Houde, 1972), and salinities have ranged from 29 to 37‰. Larvae and juveniles up to 38.7 mm standard length are included in this description, but we have reared scaled sardines to more than 100 mm in some experiments.

Morphometrics

Eggs and larvae were measured with an ocular micrometer in a dissecting microscope. The following measurements were made:

Total length (TL)—Tip of snout to end of caudal fin.

Standard length (SL)—Tip of snout to tip of notochord on small larvae, before notochord flexure; tip of snout to base of hypural plate on larger larvae, after notochord flexure. Unless otherwise noted, all references to lengths of larvae in text refer to standard lengths.

Preanus length—Tip of snout to anus, measured along midline. This measurement is equivalent to preanal fin length for specimens that have the anal fin developed.

Predorsal length—Tip of snout to origin of dorsal fin, measured along midline of body.

Prepelvic length—Tip of snout to origin of pelvic fins, measured along midline of body.

Head length—Tip of snout to posterior margin of otic capsules in yolk-sac larvae; tip of snout to opercular margin in older larvae.

Snout length—Tip of snout to anterior margin of eye.

Eye diameter—Horizontal distance between anterior and posterior edges of the fleshy orbit.

Body depth—Vertical height of the body at the pectoral symphysis.

Meristics

Fin rays were counted in each of the developing fins (Table 4). Myomeres were counted and designated as follows:

Total myomeres.

Preanal myomeres: number anterior to the anus.

Postanal myomeres: number posterior to the anus.

Predorsal myomeres: number anterior to the dorsal fin origin.

Postdorsal—preanal myomeres: number between the posterior insertion of the dorsal fin and the anus.

Osteology

Sequence of ossification was determined from a total of 16 specimens ranging in length from 4.8 to 22.4 mm. They were cleared with trypsin and stained with alizarin using the method of Taylor (1967). Development of the caudal fin bones was examined in detail. Ossification of fin rays, vertebrae, and head bones also was examined.

DESCRIPTION

Description and Occurrence of Embryos

Ten fertilized eggs from plankton collections were spherical, ranging from 1.55 to 1.78 mm in diameter (mean = 1.66 mm). They had a single, light yellow oil globule ranging from 0.07 to 0.10 mm in diameter (mean = 0.09 mm). Measurements did not differ from artificially fertilized eggs described by Matsuura (1972). Embryos were well developed when preserved (Figure 6A), and yolk diameters ranged from 0.63 to 0.72 mm at that time. The perivitelline space was wide, averaging 58% of the egg diameter for the 10 preserved specimens. In living embryos, the yolk is clearly segmented, but segments are difficult to see in preserved specimens. The chorion is thin, unpigmented, and unsculptured; it is fragile and easily broken compared to most teleost eggs. Preserved embryos had no discernible pigment. Living embryos, just prior to hatching, had tiny melanophores, which were difficult to see, in a paired dorsolateral series near the dorsal midline.

Embryos that were collected from mid-May through July were well developed by noon when our collections were examined (Figure 7). Surface water temperatures were 28°C or higher in the spawning area. Spawning presumably occurs only at night because embryos are all at similar stages of development when collected in the morning. Hatching usually began by late after-

noon, less than 24 h after the presumed spawning time.

The spawning season extends from February through July near Miami, based on our collections of planktonic eggs. Spawning may occur within Biscayne Bay from late February through early May but is confined to more offshore areas later in the season. Biggest egg collections were made about 4 km east of Miami Beach during May and June. Martinez (1972) confirmed the spawning season of scaled sardines by determining gonad indices and examining ovarian maturation of adults collected throughout the year from south Florida.

Description of Larvae

Body Shape

Larvae were 2.4 mm at hatching. The head was bent over the large, nearly spherical yolk sac. Yolk was absorbed and the body axis straightened during the next 12 h at 26° to 28°C. By 12 to 15 h after hatching, larvae were typically clupeoid (Figure 8A). They were elongate, thin larvae averaging 4.4 mm at 15 h after hatching. The gut was a long straight tube at this stage. Little growth occurred during the first 3 days after hatching. Thereafter, growth was rapid and temperature-dependent (Saksena et al., 1972). Larvae retained the typically elongate and rodlike shape until they transformed to juveniles when they became deeper bodied and laterally compressed. Proportional measurements of larvae in relation to standard length are given in Table 1.

Yolk Absorption and Gut Differentiation

Absorption of the nearly spherical yolk mass in newly hatched larvae was rapid at 26° to 28°C. The oil globule was located ventrally and just posterior to the middle of the yolk mass in newly hatched larvae (Figure 8A). By 48 h after hatching the yolk sac and oil globule had been absorbed, and larvae were actively feeding. The gut was a straight tube at 15 h after hatching (Figure 8A), but a distinct foregut and hindgut were present at 2 days (Figure 8B). By 4 days (at about 5.0 mm) the hindgut appeared to be composed of a series of adjacent muscular rings, typical of clupeid larvae.

Total Length and Standard Length

Standard length was used to examine development of scaled sardine larvae with respect to other morphometric data. The relation between standard length and total length (Table 1, Figure 1) was not linear over all sizes of larvae that were available. Standard length decreased relative to total length as larvae grew. Standard length was about 97% TL for larvae between 4 and 8 mm TL but decreased to 85% TL for larvae between 8 and 25 mm TL. The ratio averaged about 83% TL for individuals longer than 25 mm TL. The observed decrease between 8 and 25 mm TL was related to development of the caudal fin, particularly notochord flexure and hypural plate development.

Preanus Length

Preanus length averaged 83% SL at 15 h after

TABLE 1.—Summary of relationships between total lengths (TL) and standard lengths (SL), and proportional measurements relative to standard lengths for larvae used to describe *Harengula jaguana* development. Proportions are from data fitted by eye to relationships in Figures 1 to 5.

TL (mm)	SL (mm)	SL:TL	Preanus length: SL	Predorsal length: SL	Body depth: SL	Head length: SL	Snout length: SL	Eye diameter: SL	Prepelvic length: SL
4.3	4.2	0.977	0.833	—	0.064	0.119	0.017	0.045	—
6.2	6.0	.968	.867	—	.067	.133	.025	.042	—
8.2	8.0	.978	.888	0.680	.064	.138	.031	.041	—
10.8	10.0	.926	.890	.648	.081	.157	.036	.041	—
13.0	12.0	.923	.900	.626	.087	.167	.040	.043	0.440
15.4	14.0	.909	.864	.600	.100	.185	.047	.050	.447
18.5	16.0	.865	.838	.556	.125	.204	.052	.056	.466
20.8	18.0	.865	.822	.517	.142	.217	.057	.057	.467
23.1	20.0	.866	.780	.478	.162	.240	.066	.064	.462
25.6	22.0	.859	.764	.441	.184	.264	.072	.073	.465
29.0	24.0	.828	.775	.417	.219	.262	.072	.075	.482
31.5	26.0	.825	.758	.404	.236	.260	.072	.077	.485
33.6	28.0	.833	.750	.408	.245	.257	.071	.075	.481
36.0	30.0	.833	.750	.410	.252	.257	.071	.074	.482
38.5	32.0	.831	.750	.409	.262	.250	.071	.073	.482

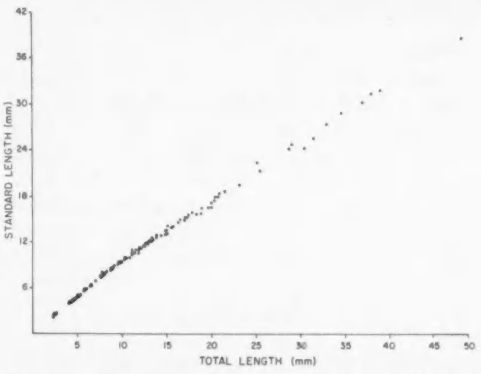

FIGURE 1.—Relation between standard length and total length for larvae of *Harengula jaguana*.

hatching and increased to about 90% SL when larvae were 12 mm (Table 1, Figure 2). A gradual decrease in preanus length occurred in larger larvae. At 22 mm, preanus length was 76% SL; juveniles 28 to 32 mm had preanus lengths that averaged 75% SL. Decreasing preanus length in larger larvae was caused by shortening of the gut during transformation to the juvenile stage.

Head Length

Head length increased relative to standard length from 12% at 4.2 mm to 26% at 22.0 mm (Table 1, Figure 3). The ratio was constant at 25 to 26% SL for specimens between 22 and 38.7 mm, which falls within the range of variation in head lengths reported for juvenile and adult *H. pensacolae pensacolae* (Rivas, 1950).

Eye Diameter

Eye diameters averaged 4.0 to 4.5% SL for specimens 4.2 to 12 mm (Table 1, Figure 4). A rapid increase in eye diameters from 4.3 to 7.3% SL occurred in specimens 12 to 22 mm. Eye diameters on specimens longer than 22 mm varied, but no increasing trend relative to standard length was observed. A 38.7-mm specimen had an eye diameter of 7.8% SL. Eye diameters were variable for larvae of a given length (Figure 4); for example, at 12 mm, eye diameters varied from about 3.5 to 5.5% SL. Rivas (1950) and

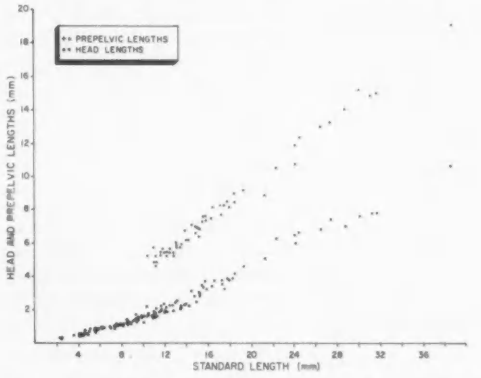

FIGURE 3.—Relation of head length and prepelvic length to standard length for larvae of *Harengula jaguana*.

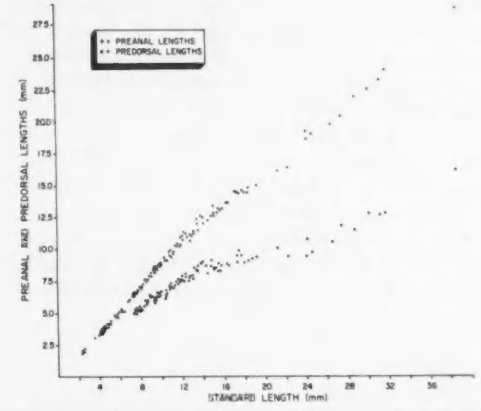

FIGURE 2.—Relation of preanal length and predorsal length to standard length for larvae of *Harengula jaguana*.

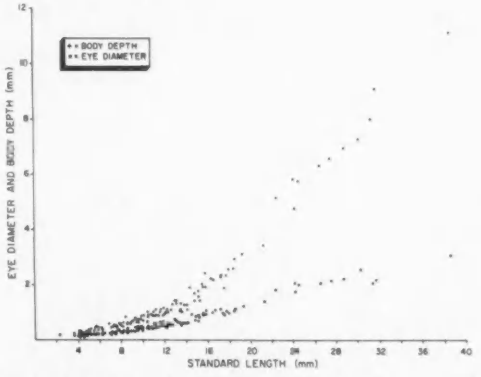

FIGURE 4.—Relation of eye diameter and body depth to standard length for larvae of *Harengula jaguana*.

Storey (1938) found eye diameters to be variable for juvenile and adult *H. pensacolae*.

Snout Length

Snout length increased from 1.7 to 7.2% SL for larvae between 4.2 and 22.0 mm (Table 1, Figure 5). It remained constant for longer larvae at about 7.2%, which is within the range of variation for juvenile and adult *H. pensacolae* (Rivas, 1963). Like eye diameters, snout lengths varied considerably for larvae of a given size; for example, at 12 mm, snout length varied from about 3.1 to 4.8% SL.

Body Depth

Body depth at the pectoral symphysis was constant at about 6.5% SL for larvae from 4.2 to 9.0 mm. Body depth then increased rapidly from 7.0 to 21.9% SL for specimens between 9.0 and 24.0 mm SL. A slow increase continued to occur for larger individuals (Table 1, Figure 4).

Predorsal Length

Predorsal lengths, as measured from the snout to the first developing ray in the dorsal fin, were recorded on specimens 7.5 mm and longer, when the rays began to develop. The dorsal fin moves forward as development proceeds, causing predorsal length to decrease from 68.0% SL to 41.7% SL for larvae between 7.5 and 24.0 mm (Table 1, Figure 2). Predorsal lengths averaged 41% SL for specimens longer than 24.0 mm.

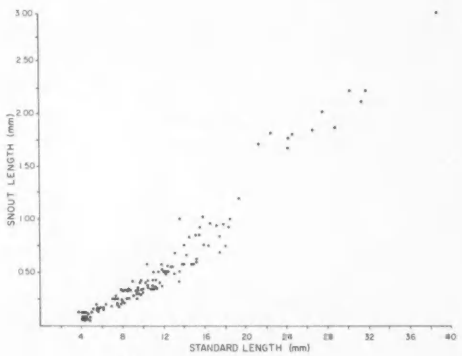

FIGURE 5.—Relation of snout length to standard length for larvae of *Harengula jaguana*.

Prepelvic Length

Prepelvic lengths were measured on larvae that had pelvic fin buds or fins. At 11 to 12 mm, prepelvic lengths averaged about 44% SL, increasing to 46% SL for larvae up to 22 mm (Table 1; Figure 3). Prepelvic lengths averaged 48% SL for specimens between 24 and 38.7 mm. Pelvic fins moved slightly posterior as larvae transformed to juveniles, causing the observed small increase in prepelvic length.

Meristics

Myomeres

Total numbers of myomeres ranged from 39 to 42; most larvae had 40 or 41. Numbers of myomeres and distribution of myomeres in relation to other body parts can be useful for identifying clupeid genera (Ahlstrom, 1968). Total myomeres could be counted accurately on 144 of our larvae. Frequencies were as follows:

Number of myomeres	39	40	41	42
Frequency	2	68	67	7

The mean number of myomeres was 40.56 ($S_{\bar{x}} = 0.2861$).

Distribution of myomeres in relation to the dorsal fin and anus was examined for larvae in 2-mm size classes (Table 2). Preanal myomeres decreased as larvae grew from about 35 for the smallest larvae to 27 at transformation. Postanal myomeres increased from a mean number of 5.7 for the smallest larvae to more than 12 for transformed specimens. Shortening of the gut during development accounted for the observed changes in preanal and postanal myomere counts. Mean numbers of predorsal myomeres decreased rapidly from about 25 to 10 as development proceeded, reflecting the anterior movement of the dorsal fin. Considerable variation in predorsal myomere numbers was present for larvae of a given length (Table 2). Postdorsal-preanal myomeres ranged from 5 to 7 for larvae of all sizes, but the mean number tended to decrease as larvae grew from 8 to 22 mm.

Fin Development

Newly hatched larvae had a fin fold that invested much of the body and which persisted in

TABLE 2.—Distribution of myomeres relative to other body parts for *Harengula jaguana* larvae.

Size class (mm, SL)	Preanal myomeres			Postanal myomeres			Predorsal myomeres			Postdorsal-preanal myomeres		
	Number of specimens	Mean	Range	Number of specimens	Mean	Range	Number of specimens	Mean	Range	Number of specimens	Mean	Range
4.0- 6.0	34	34.85	34-36	36	5.67	5-7	—	—	—	—	—	—
6.1- 8.0	16	35.00	34-36	17	5.53	5-7	11	24.82	23-26	12	6.67	5-7
8.1-10.0	22	34.68	33-36	22	6.09	5-7	22	23.41	22-25	22	6.50	5-7
10.1-12.0	18	33.72	32-35	18	6.89	6-8	18	21.61	20-24	18	6.00	5-7
12.1-14.0	15	33.47	32-35	15	7.20	6-8	15	21.07	20-23	15	5.67	5-7
14.1-16.0	12	32.08	30-34	12	8.25	7-9	12	18.75	16-22	12	5.42	5-6
16.1-18.0	6	31.67	31-33	6	8.50	8-9	6	17.17	16-19	6	5.50	5-6
18.1-20.0	4	31.00	31	4	9.25	9-10	4	15.25	15-16	4	5.50	5-6
20.1-22.0	1	29.00	29	1	11.00	11	1	13.00	13	1	5.00	5
>22.0	4	27.25	26-28	4	12.75	12-14	4	10.00	8-11	4	6.25	6-7

part until larvae were about 16 mm. Pectoral fin buds were present at hatching (Figure 8A), but no other fins were developed at this stage. An opaque area in the fin fold was the first indication of median fin development. Rayed fins developed in the following sequence: dorsal, caudal, anal, pelvics, pectorals. Fin rays first develop as cartilaginous structures; thus, the sizes of larvae at which full complements are present may be smaller than the sizes at which rays are fully ossified. Tables 3 and 4 summarize fin development sequence of scaled sardine larvae, and details are discussed in the osteological development section.

Median fin development usually was completed at 16.0 mm. Dorsal fin rays first appeared between 7.0 and 7.5 mm. A full complement of 17 to 19 rays was present at 14.0 to 17.0 mm. Principal caudal rays were first seen at 7.4 to 8.0 mm, and the full complement of 19 usually was attained at 10.0 mm. Some specimens as small as 8.5 mm had the full complement of principal caudal rays; a few specimens did not have a full complement until they were longer than 11.0 mm. Secondary caudal rays developed at 10.8 to 12.8 mm, and the full complement of 8 or 9 dorsal and 7 ventral secondary caudal rays was present at 16.5 to 19.0 mm. Notochord flexure, which occurs during caudal fin development, began at the same size that principal caudal rays first developed. Anal fin rays usually began to develop at 9.0 to 9.3 mm, but two specimens 8.5 to 9.0 mm had some anal rays. A full complement of 17 or 18 anal rays was present at 13.0 to 15.0 mm. Although principal caudal and anal fin rays began to develop after dorsal fin rays, the dorsal was the last median fin to attain its full ray complement.

Paired fins began to develop after median

TABLE 3.—Summary of fin development sequence in larvae of *Harengula jaguana*.

Fin	Buds first appear	Standard length (mm)[1]		Number of rays in fully developed fin
		Rays first appear	Full complement of rays	
Dorsal	—	7.0 to 7.5	14.0 to 16.0	17 to 19
Caudal				
Principal	—	7.4 to 8.0	8.5 to 11.0 (most by 10.0)	19
Secondary	—	10.8 to 12.8	16.5 to 19.0	8 or 9 dorsally 7 ventrally
Anal	—	9.0 to 9.3 (rarely at 8.5 to 9.0)	13.0 to 15.0	17 or 18
Pelvic	11.0-12.0 (rarely at smaller size)	13.0 to 14.0 (rarely at <13.0)	14.6 to 17.8 (most by 15.5)	7 or 8 (usually 8)
Pectoral	<4.0	15.0 to 16.0 (rarely at smaller size)	18.5 to 19.5	14 to 16

[1]Rays were present at the tabulated lengths, but not necessarily ossified at those sizes.

TABLE 4.—Some meristic characters of larval and juvenile *Harengula jaguana*.

Standard length (mm)	Caudal rays	Dorsal rays	Anal rays	Pectoral rays	Pelvic rays
2.3-6.9	No elements present on 48 specimens in this size range				
7.0	—	5	—	—	—
7.3	No elements present on this specimen				
7.4	3	6	—	—	—
7.4	—	6	—	—	—
7.5	—	8	—	—	—
7.5	—	3	—	—	—
7.6	No elements present on this specimen				
7.6	—	9	—	—	—
7.7	—	7	—	—	—
7.8	2	9	—	—	—
7.9	3	8	—	—	—
7.9	5	9	—	—	—
8.0	—	8	—	—	—
8.0	2	5	—	—	—
8.1	3	6	—	—	—
8.3	6	11	—	—	—
8.5	19	14	3	—	—
8.6	6	11	—	—	—
8.6	10	11	—	—	—
8.6	—	2	—	—	—
8.9	4	8	—	—	—
9.1	15	8	—	—	—
9.1	15	12	5	—	—
9.4	8	12	3	—	—
9.4	19	12	8	—	—
9.4	19	13	5	—	—
9.4	10	9	3	—	—
9.5	15	10	—	—	—
9.5	3	9	—	—	—
9.7	19	12	8	—	—
9.7	19	12	8	—	—
9.8	19	14	6	—	—
9.8	17	13	7	—	—
9.8	19	12	6	—	—
10.0	19	14	9	—	—
10.0	8	10	—	—	—
10.4	19	14	9	—	—
10.4	18	16	15	—	—
10.5	19	15	10	—	—
10.5	19	13	10	—	—
10.9	14	11	2	—	—
10.9	19	16	12	—	—
11.0	17	14	3	—	—
11.0	17	9	3	—	—
11.2	19	14	11	—	—
11.3	19	16	12	—	—
11.3	19	15	11	—	—
11.5	19	13	10	—	—
11.7	19	17	4	—	3
11.7	19	13	9	—	—
11.9	19	14	13	—	—
11.9	19	16	15	11	5
12.0	19	14	10	—	—
12.1	19	14	8	—	—
12.2	19	16	13	—	—
12.3	19	15	9	—	—
12.4	19	14	8	—	—
12.7	19	15	12	—	—
12.8	19	15	12	—	—
12.8	19	15	10	—	—
13.0	19	17	17	9	5
13.1	19	17	16	—	2
13.1	19	17	15	—	6
13.5	19	14	11	—	—
13.6	19	15	9	—	—
13.7	19	16	12	—	—
13.9	19	17	11	—	—
14.0	19	16	12	—	—
14.2	19	16	14	—	—
14.6	19	17	17	12	7
14.9	19	16	16	—	4
14.9	19	17	16	—	6
15.2	19	17	17	—	7
15.2	19	17	17	5	6
15.2	19	18	15	—	3
15.5	19	17	15	10	8
15.6	19	18	15	10	7
15.8	19	17	17	13	7
15.9	19	17	17	—	7
16.4	19	18	17	11	7
16.6	19	17	17	12	8
17.3	19	19	17	14	8
17.4	19	19	17	13	8
17.5	19	18	17	—	6
17.8	19	18	17	12	6
18.0	19	18	17	12	7
18.4	19	18	18	13	8
18.6	19	18	16	15	7
19.3	19	17	17	14	8
21.3	19	18	17	15	8
22.4	19	17	17	14	8
24.2	19	17	18	14	8
24.2	19	18	17	15	7
24.7	19	18	18	14	7
26.7	19	17	18	14	8
27.5	19	18	18	15	7
28.9	19	17	18	15	8
30.2	19	17	18	15	8
31.4	20	18	17	16	8
31.8	19	17	18	14	8
38.7	19	17	17	15	7

fins. Rayless pectoral fins were present soon after hatching, but rays usually did not develop until larvae were 15.0 to 16.0 mm. One specimen had some pectoral rays at only 11.9 mm, but this was unusual. Full complements of 14 to 16 pectoral rays were attained at 18.5 to 19.5 mm. Pectorals were the last fins to complete development. Pelvic fins first appeared as buds when larvae were 11.0 to 12.0 mm; most specimens had pelvic buds at 11.3 mm. Pelvic rays usually began to develop at 13.0 to 14.0 mm, but one 11.7-mm specimen had rays. A full complement of 7 or 8 (usually 8) pelvic rays was present at 14.6 to 17.8 mm. Most specimens had complete pelvic fins by 15.5 mm.

Scales

Scale development apparently occurred at 21 to 22 mm. No specimens from 18.5 to 21.2 mm were scaled. The illustrated specimen 21.3 mm (Figure 10C) was fully scaled as were 4 specimens from 22.4 to 24.2 mm.

Osteological Development

Sixteen cleared and stained specimens provided a record of sequence of development of skeletal structures in scaled sardine larvae. Bones stain as a result of calcification, but many bones, though unstained, were discernible before

calcification as distinct cartilaginous structures. Our four smallest specimens (4.8, 6.2, 6.5, and 8.9 mm) showed no evidence of staining and only slight indication of developing bone structures. Our first specimen to show clear evidence of stain uptake and well-formed cartilaginous structures was 10.9 mm. The only bone which was stained in this specimen was the cleithrum. The next bones to stain (an 11.5-mm specimen) were the maxillaries, dentaries, principal caudal fin rays, hypurals, and parhypural. Ossification then proceeded rapidly as larvae grew.

The Caudal Fin Complex

Clupeids have a complex caudal fin, and for descriptive purposes we follow the terminology of Nybelin (1963). The adult caudal fin has the following structures: 2 ural vertebrae, 6 hypurals, a parhypural associated with the first preural vertebra, 19 principal caudal rays (the lower and upper are unbranched, the remainder branched), 2 or 3 epurals, 3 pairs of uroneurals, 8 or 9 dorsal secondary caudal rays, 7 ventral secondary caudal rays, and a modified neural arch and spine on the first preural vertebra. In a 9.9-mm specimen the parhypural and the first four hypurals were visible (but not stained) as distinct cartilage entities (Figure 6A). A noticeable gap was present between the second and third hypural which persisted to the adult stage and separated the 9 lower from the 10 upper principal caudal rays.

The association of individual principal caudal fin rays with the parhypural and hypurals was nearly constant. Our method of counting principal caudal rays was anterior to posterior or, after notochord flexion, ventral to dorsal. The hypurals were counted similarly. The first two principal rays articulated with the parhypural, rays 3 to 7 articulated with the first hypural (in specimens larger than 15.0 mm ray 8 also associated with this hypural); rays 8 and 9 with the second hypural; rays 10 to 14 with the third hypural; rays 15 and 16 with the fourth hypural; rays 17 and 18 with the fifth hypural; and ray 19 with the sixth hypural. Rays 1 and 19 were stained deepest, and staining decreased medially indicating that rays 9 and 10 were the last to ossify although these rays were the first to develop.

In the 11.5-mm specimen (Figure 6B) there was a slight indication of ossification of the first pair of uroneurals and the neural arch of the first preural vertebra. The hypurals were all stained as was the parhypural and hemal spine of the second preural vertebra. In the 11.9-mm specimen the first uroneural pair was well stained as was the second uroneural pair, and the second ural centrum was deeply stained. The second uroneural lay just posterior to the second ural vertebra along the plane of the notochord. The first uroneural originated above an area that became the first preural centrum, but there was no indication of the centrum at 11.9 mm. The first uroneural extended along the notochord over the second ural centrum and ended midway along the second uroneural. The second uroneural extended from the second ural centrum to the origin of the sixth hypural. Two other structures were discernible but not stained at 11.9 mm—the hemal spines of the second and third preural vertebrae and the posteriormost ventral secondary caudal fin ray.

In the 12.0-mm specimen, little change occurred. In the 12.4-mm specimen, all the structures mentioned above were more deeply stained, and the neural and hemal spines of the second preural vertebra (though this vertebra is undifferentiated) were stained (Figure 6C). Of particular interest in this specimen was the marked similarity of the hemal spine of the second preural vertebra to the parhypural. Nybelin (1963) considered the parhypural to be a hemal spine, and our observation bears this out in as much as the caudal artery goes through this bone rather than over it. Monod (1968) has referred to the hemal spine of the first preural centrum as the parhypural bone and Hollister (1936) considered this bone to be a hypural. We use the term parhypural because it has characteristics of both a hypural bone and a hemal spine. During its development, it closely resembles a hypural and in fact is joined to the first hypural (see Figure 6D), and it bears two principal caudal rays. Both spines of the two preural vertebrae are flattened bones with developing hemal arches between the spine base and the notochord. In the 14.0-mm specimen, the first preural centrum and the two ural centra were stained as was the lower portion of the second preural centrum. The posteriormost ventral secondary caudal ray was stained. A neural arch was visible, though unstained on the first pre-

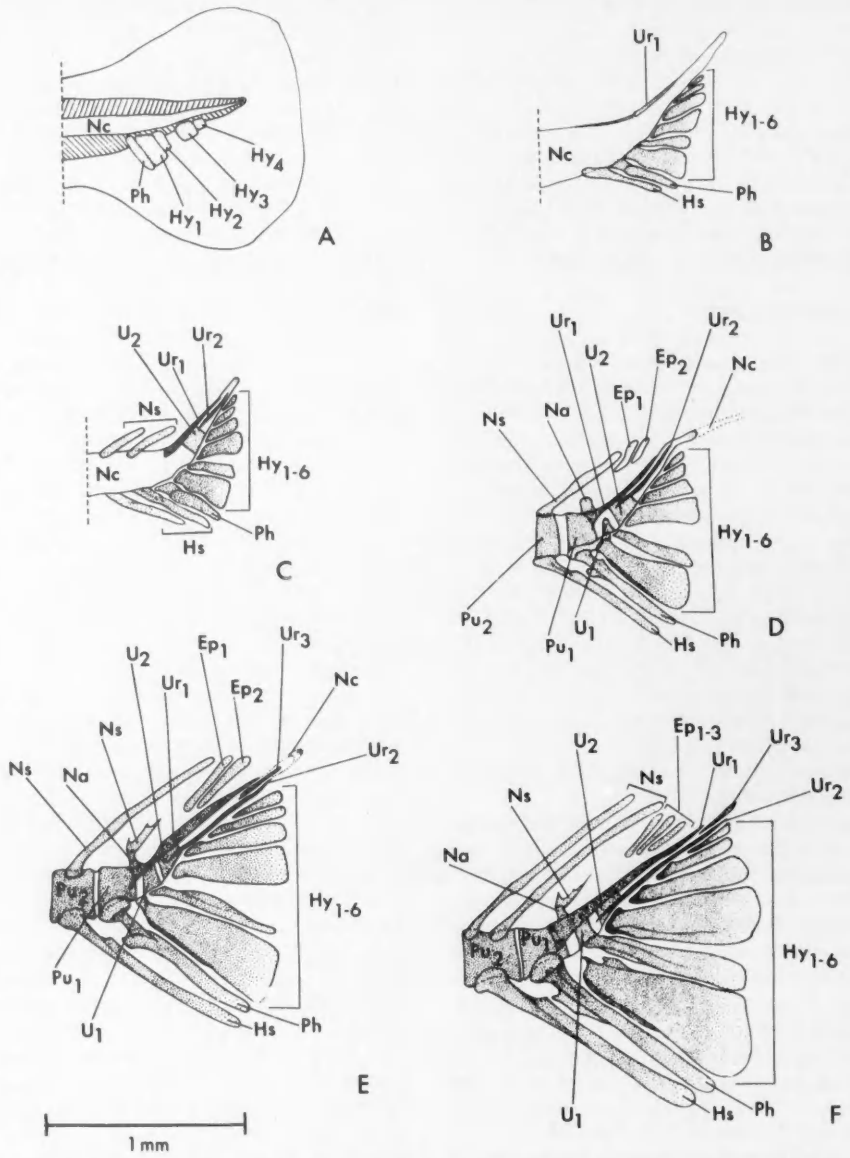

FIGURE 6.—Development of the caudal fin structures in larvae of *Harengula jaguana*. Fin rays are omitted from the illustrations to show the supporting structures more clearly. Standard length of specimens: A, 9.9 mm; B, 11.5 mm; C, 12.4 mm; D, 14.9 mm; E, 18.0 mm; F, 19.3 mm. Abbreviations: HY_{1-6} = hypurals, Ep_{1-3} = epurals, U_1 and U_2 = ural vertebrae, P_{U1} and P_{U2} = preural vertebrae, Hs = hemal spine, Nc = notochord, U_{r1}-U_{r3} = uroneurals, Ns = neural spine, Na = neural arch, Ph = parhypural.

ural centrum and was not connected to the first uroneural base.

In the 14.9-mm specimen major features included an ossified area on the notochord posterior to the sixth hypural (Figure 6D). This structure apparently was temporary; it was not the third uroneural and it was not as clearly observed in larger specimens. Four upper secondary caudal rays were visible though only the posteriormost was stained. Three lower secondary caudal rays also were present with only the posteriormost stained. Two epurals were barely discernible and were not stained. The "hemal archlike" bone of the parhypural changed shape and appeared as a forked bone which received the spine of the parhypural between its forks. This small hemal archlike bone also supported the first hypural and abutted the first preural centrum, the notochord between the first preural centrum and the first ural centrum, and the first ural centrum itself. The third hypural abutted the second ural centrum, and the remaining hypurals abutted the notochord. At this stage, it was obvious that the first uroneural was fused to the first preural centrum. The second uroneural was free and never fused with any bone.

In the 15.6-mm specimen, seven upper secondary caudal rays and four ventral secondary caudal rays were stained. Two epurals were visible but weakly stained. An anteriorly directed flange or expansion had developed on the base of the parhypural. Its supporting hemal arch structure was distinct and not fused with the flange. The neural arch on the first preural vertebra was beginning to ossify. In the 16.6-mm specimen, the third uroneural was visible, lying lateral to the second uroneural. It was shaped like the second uroneural but was much smaller and appeared as a well ossified splintlike bone. The ossified area above the sixth hypural that was noted in the 14.9-mm specimen was not present. Three epurals were visible but not ossified. The full complement of secondary caudal rays was present—eight upper, seven lower.

In the 18.0-mm specimen, several significant changes were evident (Figure 6E). First, only two epurals were present, and they were slightly stained. This probably was the result of individual variation since three were observed in the 16.6-mm specimen. The neural arch of the first preural vertebra had developed an upward projecting spinelike process. This neural arch lay over the posterior dorsal surface of the first preural centrum between the bases of the left and right first uroneural. We did not verify that the dorsal nerve passes through this arch; thus this neural arch and spine of the first preural vertebra could be some other bone. Fusion had not taken place between the neural arch and the first uroneural bases in this specimen. The first hypural no longer touched the first preural centrum, and a remnant of its hemal archlike base remained between the vertebra and the hypural. The first or anteriormost upper and lower secondary caudal fin rays lay parallel to the body axis rather than slightly vertical as in smaller specimens. The third uroneural lay immediately above and posterior to the second uroneural.

Little difference was noted between the 19.3-mm and the 18.0-mm specimen except for the complete absence of the hemal archlike support of the first hypural in the larger specimen (Figure 6F). Three epurals were present but were still only faintly stained. Without doubt, these were the last components of the caudal fin to ossify. In this specimen, there were nine upper and seven lower secondary caudal rays. The second preural vertebra had the anomalous condition of bearing two neural spines.

All three uroneurals are paired and obviously provide rigid support for the notochord as the tail develops. As a result, the first and second uroneurals are among the first tail bones to ossify. The ossified first uroneural fuses to the first preural centrum after the centrum becomes ossified. The other uroneurals were not fused to any bone in the *Harengula* we examined nor were they fused to other bones in large larvae of *Opisthonema* (Richards, Miller, and Houde, 1974).

Dorsal and Anal Fins

Ossification of dorsal fin rays was first observed in the 11.9-mm specimen. Twelve rays in the midregion of the developing fin were faintly stained. Supporting pterygiophores for these rays also were faintly stained. About eight unstained anal rays were visible, but no supporting pterygiophores were seen. In the 12.4-mm specimen, 12 dorsal rays also were stained but these were the last 12 rays of the fin. Supporting pterygiophores for these rays also were stained.

The anal fin rays showed only slight staining. The 14.0-mm specimen had 15 ossified dorsal rays and pterygiophores; the anal had 11 unstained rays and pterygiophores. At this size, the vertebrae were countable and the dorsal rays were over the 24th to 29th vertebrae. The anal fin was beneath the 34th to 38th vertebrae. In the 14.9-mm specimen, 17 ossified dorsal rays were present and were over the 20th to 27th vertebrae. The anal fin had 15 faintly stained rays and visible but unstained pterygiophores. This fin was under the 33rd through 38th vertebrae. In the 15.6-mm specimen, the anal fin pterygiophores were well ossified. Seventeen dorsal pterygiophores supported 18 rays (1 pterygiophore supported the first 2 rays), and 14 anal pterygiophores supported 15 ossified anal rays (1 pterygiophore supporting the first 2 rays). In that specimen, the dorsal fin was over the 19th to 27th vertebrae, the anal under the 33rd to 37th vertebrae. In the 16.4-mm specimen, 18 dorsal and 16 anal ossified rays were present. The first few pterygiophores of each fin were faintly stained. The dorsal fin was over the 18th to 25th vertebrae, the anal under the 32nd to 38th vertebrae. In the 18.0-mm specimen, there were two ural vertebrae in the caudal region. In the 12.0-mm specimen, the middle vertebrae were visible because the ventral portions of their centra were ossified. In the 12.4-mm specimen, 20 vertebrae anterior to the dorsal fin were ossified. Neither the first few vertebrae nor the last several were ossified. The 14.0-mm specimen had the first vertebra faintly stained, the next 36 were complete, the next 3 were visible but unstained, and the last had only the lower half of the centrum stained. In this specimen, a few neural arches near the middle of the vertebral column were lightly stained. The first 10 hemal spines also were slightly stained as were the 2 preceding the parhypural. In the 14.9-mm specimen, all neural spines and hemal spines were lightly stained. Pleural ribs were first observed in the 15.6-mm specimen on the 8th to 16th vertebrae. From density of stain, it appears that they develop in a posterior to anterior direction.

Head Bones

The many skull bones were difficult to describe. A detailed analysis of general developmental changes in skull development has been completed for the related Atlantic thread herring, *Opisthonema oglinum* (Richards et al., 1974). The maxillaries and dentaries of scaled sardines ossified at 11.5 mm. At this time, the maxillary bore five small teeth. These teeth were too small to be shown in the illustrations. Teeth were added with growth—8 teeth at 14.0 mm, 14 teeth at 14.9 mm, 17 teeth at 15.6 mm. Teeth were observed on the dentary only on the 15.6-mm specimen, where two were observed. Dentary teeth apparently are a temporary feature. Teeth also were present on the basihyal; the 15.6-mm specimen had two large teeth, and the 16.6-mm specimen had three teeth on this bone. These teeth, like the dentary teeth, apparently are temporary larval structures. They were also seen as temporary structures in the larvae of *O. oglinum* (Richards et al., 1974). The premaxillaries were first visible in the 14.9-mm specimen, and the posterior supramaxillaries were first seen in the 16.6-mm specimen. The anterior supramaxillaries and the hypomaxillaries had still not developed in our 19.3-mm specimen but were present in our 22.4-mm specimen. Berry (1964a) reported hypomaxillaries to be developed in a 16-mm specimen of *Harengula thrissina* from the eastern Pacific.

Pigmentation

Melanophore distribution on preserved scaled

FIGURE 7.—Late stage egg of *Harengula jaguana*.

sardine larvae is similar to that of other clupeid larvae. Pigmentation varied somewhat among individuals of the same size, but a general pattern was always present. Some variation resulted because individual melanophores could be in either a contracted or expanded state. Illustrated specimens have pigmentation that is typical of most larvae of those sizes (Figures 8 to 10). In life, numerous yellow chromatophores were present, usually as internal pigmentation, but these were not illustrated.

Head Region

Pigmentation was sparse on the head of scaled sardine larvae until they attained 15 mm. Eyes became pigmented when larvae were 4 to 5 mm, at 30 to 40 h after hatching. At the same time, from two to four melanophores developed near the pectoral symphysis. These usually consisted of one just anterior to the symphysis and a pair immediately posterior to it. They were retained throughout larval development. One or two melanophores usually were present at the base of the pectoral fins when larvae were 6.5 mm or longer. From one to four stellate melanophores first appeared over the hindbrain at 7 to 8 mm. This number gradually increased as larvae grew, but some specimens had only a single melanophore at 14 mm. On specimens longer than 15 mm, melanophores became numerous over the midbrain and hindbrain. One or two deeply imbedded melanophores were visible through the otic capsules on most specimens longer than 8 mm. One or two stellate melanophores frequently appeared on the cheek when larvae were 14 mm. This number often increased to several at 15 to 18 mm. Tiny melanophores developed on the snout and lower jaw of larvae that were 14 to 17 mm. Melanophore numbers increased

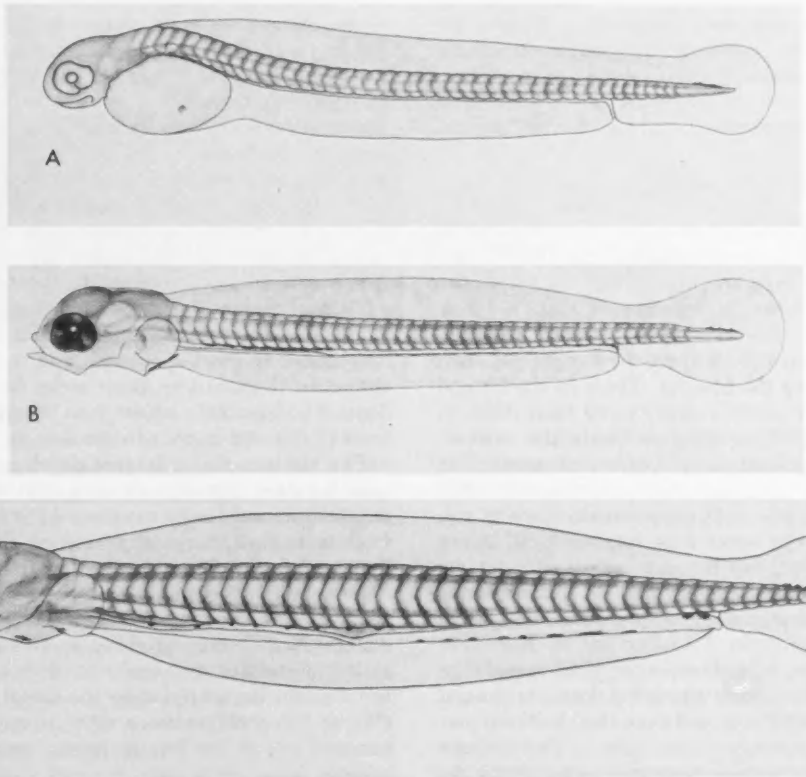

FIGURE 8.—Larvae of *Harengula jaguana*: A, 4.4 mm SL; B, 4.5 mm SL; C, 6.0 mm SL.

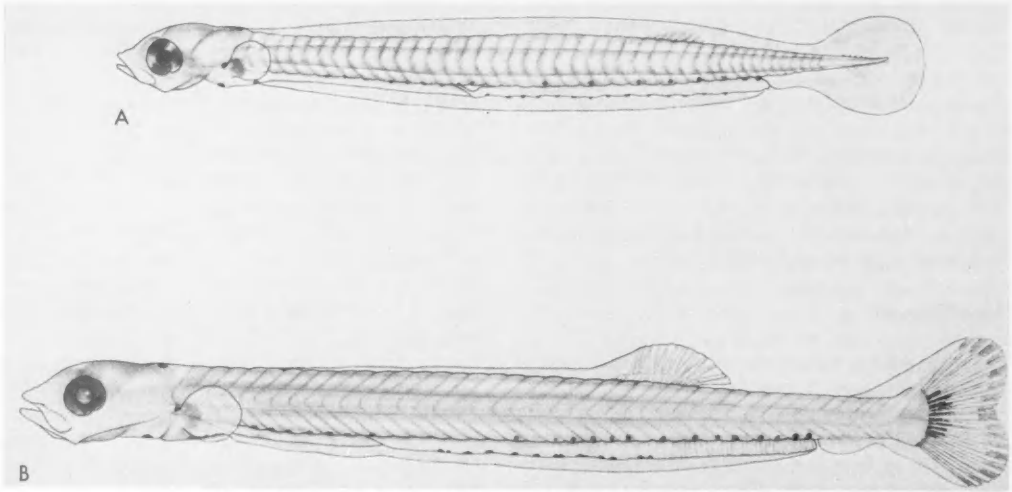

FIGURE 9.—Larvae of *Harengula jaguana*: A, 8.9 mm SL; B, 11.5 mm SL.

rapidly on specimens longer than 18 mm, although there was much individual variation. Numerous stellate melanophores were present over the brain, on the snout, jaws, and cheek region of specimens between 18 and 24 mm.

Gut and Trunk Region

Paired series of melanophores, typical of clupeid larvae, developed over the dorsolateral surface of the foregut region and along the ventral surface of the hindgut at about 4.5 mm. Numbers of pairs in the series were variable, ranging from 7 to 12 along the foregut and from 8 to 14 along the hindgut. Those on the foregut usually were more evenly paired than those on the hindgut. In specimens where the melanophores were contracted, pairs were easily distinguished, but when dispersed, the pairs often tended to coalesce forming streaky lines of pigment. The two series were retained until larvae were 21 mm, but became indistinct on some larvae between 18 and 21 mm. No distinct series could be distinguished on specimens longer than 21 mm.

Two series of melanophores were present internally. One series was found dorsal to the gut and the second extended from the hindbrain posteriorly along the vertebral column. Two melanophores appeared near the dorsal surface of the gut near the anus at 4 to 5 mm, from which the series of melanophores dorsal to the hindgut began to develop at 5 to 6 mm. The number gradually increased from as few as 2 to 5 to as many as 34 when larvae were 12 to 15 mm. The first melanophores in this series developed near the posterior of the hindgut; additional melanophores developed anterior to those. The series along the vertebral column first appeared at 10 to 12 mm, and numbers gradually increased to about 25. Melanophores in this series first appeared just posterior to the hindbrain; additional melanophores developed posterior to them. The vertebral series was difficult to distinguish in most specimens and was not included in illustrations. Both series became indistinct on specimens longer than 18 mm because larvae increased in body thickness.

Two stellate melanophores developed at the anal fin base between 11 and 13.5 mm. The number increased as larvae grew. At 14 to 15 mm, stellate melanophores appeared at the dorsal fin base, the numbers increasing from one or two to eight or more at 18 mm. Between 18 and 21 mm, a few melanophores developed in the dorsal fin of most individuals, and a paired series of stellate melanophores developed posterior to the dorsal fin along the dorsal midline. One or two melanophores were present at the bases of the pelvic fins in larvae longer than 15 mm.

Stellate melanophores began to appear on the

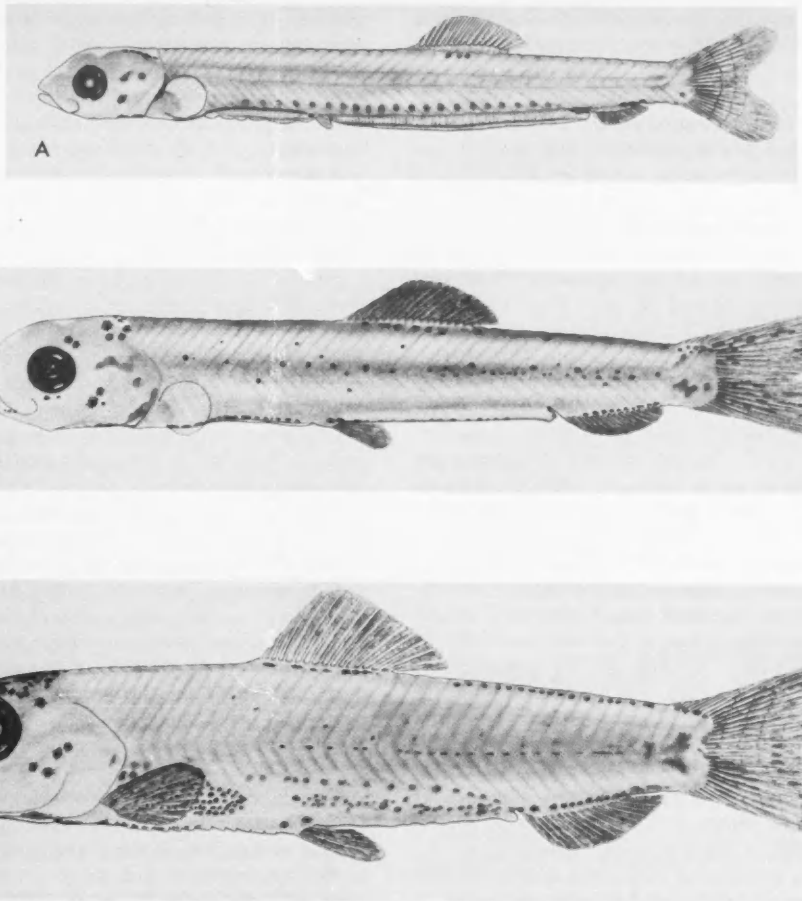

FIGURE 10.—Larvae of *Harengula jaguana*: A, 16.1 mm SL; B, 18.8 mm SL; C, 21.3 mm SL.

sides of most larvae between 16 and 17 mm. The first of these developed posterior to the dorsal fin along the lateral midline of larvae. Numbers increased as larvae grew, spreading anteriorly, dorsally, and ventrally so that most individuals had numerous melanophores scattered over their sides by 22 mm. The epaxial myomeres of specimens longer than 22 mm usually were outlined by melanophores that were concentrated along the myosepta. Silver coloration began to appear along the ventral and ventrolateral areas of the trunk at 22 to 24 mm. By 28 mm few melanophores could be discerned below the midline on sides of juveniles because of the accumulation of guanine in that area. At this stage, scaled sardines resemble large juveniles and adults because of their predominantly silver color.

Caudal Region

Newly hatched larvae, 4 to 4.5 mm, had three or four melanophores along the dorsal tip of the notochord. In the first 48 h after hatching, the number of melanophores in that area ranged from three to six. During the same time from one to three melanophores developed along the ventral tip of the notochord in some specimens. As caudal rays began to develop at 8 to 10 mm, pigment migrated from the notochord tip to the

area surrounding the rays. From one to three deeply imbedded melanophores were present near the hypural plate when larvae reached 11 to 16 mm. Larger specimens had similar pigmentation in the caudal region except that the number of melanophores surrounding the caudal rays continued to increase as larvae grew.

Transformation

Transformation of larvae apparently was complete between 22 and 24 mm. Scaled sardines of 22 mm conformed to descriptions of juveniles and adults in most respects (Storey, 1938; Rivas, 1950, 1963). Proportional measurements relating preanal length, predorsal length, head length, and eye diameter to standard length became constant at 22 to 24 mm (Table 1). Only body depth continued to increase relative to standard length for larger individuals. The slender rodlike shape of larvae was replaced by the deeper bodied, laterally compressed shape of juveniles during transformation. Also, the relation between standard length and total length became constant when scaled sardines were 22 to 24 mm (Table 1). Full fin ray complements were present by 19.5 mm (Table 3), slightly before the dorsal and anal fins had completed their movements during transformation. Scales first developed at 21 to 22 mm, and the typical silvery coloration of juveniles was apparent at 22 to 24 mm. Some outstanding features during transformation were forward movement of the dorsal fin, shortening of the gut, forward movement of the anal fin, and relative increases in head length, snout length, eye diameter, and body depth.

COMPARISONS

Eggs and larvae of scaled sardines can be distinguished from those of similar genera in south Florida marine waters. Houde and Fore (1973) have prepared a guide that will help to identify eggs and larvae of some clupeid fishes, including scaled sardines, from the Gulf of Mexico.

Scaled sardine eggs are larger than those of other clupeid genera from south Florida. Only scaled sardines have eggs larger than 1.50 mm diameter. Eggs of *Opisthonema oglinum, Sardinella anchovia, Brevoortia* spp., and *Etrumeus teres* rarely exceed 1.35 mm diameter. The oil globule of scaled sardine eggs is smaller than that reported for other clupeid genera. Eggs of *Etrumeus* have no oil globule and cannot be confused with scaled sardines. Two other species of *Harengula* may occur near Miami. *Harengula humeralis* and *H. clupeola* are not common compared to *H. jaguana*, but their eggs may be similar to those of scaled sardines. Eggs of *Jenkinsia* spp. are undescribed and cannot be compared to scaled sardine eggs.

Scaled sardine larvae can be distinguished from all other genera of clupeids with which they might cooccur, except perhaps for *Jenkinsia* spp., which are undescribed. Myomeres do not exceed 42 in *Harengula* larvae, but number 45 or more in other genera, except for *Jenkinsia* which has myomere numbers similar to *Harengula*. Larvae of *H. humeralis* and *H. clupeola* are undescribed, but probably are similar to those of scaled sardines. Caudal pigmentation of larvae less than 9 mm serves to separate scaled sardine larvae of those sizes from larvae of *Opisthonema* and *Sardinella*. Those two genera have melanophores only on the ventral side of the notochord tip while scaled sardines always have melanophores on the dorsal side of the notochord tip and frequently on the ventral side as well. *Brevoortia* larvae have caudal pigmentation like that of *Harengula*, but they rarely have fewer than 45 myomeres.

Eggs and larvae of two species that Berry (1964a) and Whitehead et al. (1966) would assign to the genus *Sardinella* have been described as *Harengula zunasi* (Uchida et al., 1958; Takita, 1966) and *H. rouxi* (Marchal, 1967). Eggs and larvae of *H. zunasi* from Japanese waters (Uchida et al., 1958; Takita, 1966) closely resemble those of *H. jaguana*. Egg diameters and oil globule diameters of *H. zunasi* average slightly larger than for *H. jaguana*, but the very wide perivitelline space and exceptionally small oil globule are similar in the two species. Pigmentation is present only on the ventral side of the notochord tip in *H. zunasi* larvae, thus differing from *H. jaguana*. Both *H. zunasi* and *H. jaguana* larvae have less than 45 myomeres—43 in *H. zunasi*, usually 40 or 41 in *H. jaguana*. Marchal's (1967) *Harengula* (= *Sardinella*) *rouxi* eggs and larvae also more closely resemble those of *H. jaguana* than other clupeid eggs and larvae that we have observed from Florida waters. Eggs of *H. rouxi* are smaller than *H. jaguana*,

but relative widths of the pervitelline space and the oil globule diameters are similar. *H. rouxi* and *H. jaguana* larvae have similar pigmentation at the notochord tip. Myomeres range from 43 to 45 in *H. rouxi*, which is higher than for *H. jaguana* but lower than the number observed in most other clupeids.

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EGG AND LARVAL DEVELOPMENT OF THE ATLANTIC THREAD HERRING, *OPISTHONEMA OGLINUM*[1,2]

WILLIAM J. RICHARDS,[3] ROBERT VICTOR MILLER,[4] AND EDWARD D. HOUDE[5]

ABSTRACT

The egg and larval development of Atlantic thread herring, *Opisthonema oglinum*, is described, based on wild-caught eggs and laboratory-reared larvae. This description includes morphological details of the egg and osteological development, changes in body shape and pigmentation, and significant features of transformation of the larval development stages. The egg is 1.10 to 1.28 mm in diameter with a single oil globule. Ossification commences in the larvae when they attain 10 mm in standard length and all bones have at least begun to ossify by 20 mm. During transformation (15 to 25 mm), the larvae assume juvenile characteristics; particularly evident during this period is the anterior movement of the dorsal and anal fins from their posterior larval positions to their medial adult positions.

The Atlantic thread herring, *Opisthonema oglinum* (Lesueur), is a clupeid fish commonly found in the subtropical and tropical waters of the western Atlantic Ocean, but the eggs and larvae of this species have not been described previously. In 1968, Atlantic thread herring were reared from eggs in the Tropical Atlantic Biological Laboratory, Miami, Fla. (now the Southeast Fisheries Center), and a complete developmental series was obtained (Richards and Palko, 1969). This paper describes the egg and morphological development of the reared larvae. We used a dynamic approach, similar to that of Moser and Ahlstrom (1970), to describe the sequential development of characters, instead of a static approach in which a few selected sizes of larvae are described in detail. Larvae reared under laboratory conditions provide unusually good specimens for studies of this kind.

The major purpose of describing eggs and larvae is to provide information so that they may be identified in field collections. Identification is very difficult among the clupeids because all of the larvae are very similar in appearance. This group is further complicated by the many species that occur. In the western North Atlantic 15 genera, representing about 36 species, are found. Three genera are distinctive since they are found in fresh water, or at least spawn and develop in fresh to brackish water. Five other genera are distinctive because of their long anal fin, and one poorly known genus because of its very few vertebrae. However, approximately 17 species remain represented by seven genera, which are very similar in appearance. These genera are *Clupea* (one species), *Etrumeus* (one species), *Jenkinsia* (three species), *Brevoortia* (four species), *Opisthonema* (two species), *Harengula* (three species), and *Sardinella* (three species). Some species within these genera are imperfectly known (Berry, 1964). At our laboratories, three other species have now been reared besides *O. oglinum*—*Sardinella anchovia, Brevoortia smithi, and Harengula jaguana*—and descriptions of these are in preparation. Except for *Sardinella*, it appears now that *O. oglinum* can be separated from all of the other genera on the basis of meristic characters. *Brevoortia* is similar in most meristic characters, but its anal fin is found nearly below the posterior end of the dorsal fin, unlike *Opisthonema*. The eggs are very similar to one another, but size and spawning times are helpful in separating the species. Much detailed work is needed to work out these identification problems, not only for the eggs and larvae but for the adults as well. A recent paper gives useful information on these identification problems (Houde and Fore, 1973).

[1]Contribution No. 236, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, FL 33149.
[2]Contribution No. 1790, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149.
[3]Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, FL 33149.
[4]Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, FL 33149; present address: National Marine Fisheries Service, NOAA, Washington, DC 20235.
[5]Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149.

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MATERIALS AND METHODS

Eggs that were used for descriptive purposes were collected in 1971 and 1972 during ichthyoplankton surveys in the eastern Gulf of Mexico. Twenty-three eggs in varying stages of development were examined and measured. Eggs from the laboratory rearing experiment were lost and consequently could not be described.

We selected only the best specimens for this study by eliminating fish with pronounced body curvature and those in poor condition. We used 53 of the 197 available specimens. Forty-two of these specimens were measured with an ocular micrometer of a dissecting microscope to provide data on body proportions. Seventeen of the specimens were cleared and stained to provide meristic data and osteological data. Specimens shown in the illustrations were among those cleared and stained for verification of the fin-ray counts. Staining procedures followed those of Taylor (1967).

During development, *O. oglinum* undergoes some pronounced changes in structure. These changes are difficult to adequately define, particularly the metamorphic stages. We have followed the definitions used by Moser and Ahlstrom (1970), and we have also taken into account Ahlstrom's (1968) comments on the subject. Our yolk-sac larvae were lost, so our description commences with the larval period. The period between the larval period and juvenile period is termed the transitional stage, following Moser and Ahlstrom (1970). At the beginning of the transitional period (about 15 mm standard length), the animals commence metamorphosis into juveniles.

Our methods of counting and measuring closely follow Moser and Ahlstrom, but for convenience are defined as follows:

Body length—In early stage larvae and in those undergoing notochord flexion, the body length is the distance from the tip of the snout to the tip of the notochord. After the hypural complex is developed the standard length measurement is used, i.e., the distance from the tip of the snout to the posterior margin of the hypural elements. While the notochord is undergoing flexion and the hypural elements are developing, this estimated standard length measurement is denoted in the tables.

Eye diameter—Maximum width of the pigmented eye measured on the horizontal axis.

Snout length—Distance from the tip of the snout to the anterior edge of the orbit.

Head length—Distance from the tip of the snout to the posterior edge of the opercle.

Length of dorsal and anal fin bases—Distance from the origin of the first ray to the point where the posterior part of the last ray contacts the body.

Snout to origin of dorsal fin—Identical to the predorsal length defined by Hubbs and Lagler (1958).

Snout to origin of pelvic fin—Distance from the tip of the snout to the pelvic fin base.

Snout to origin of anal fin—Distance from the tip of the snout to the origin of the anal fin (in small larvae, before the anal fin develops, this measurement is defined as the distance from the tip of the snout to the end of the gut; it can be used as gut length for all larvae and small juveniles).

Origin of dorsal fin to base of caudal rays—Distance from origin of the dorsal fin to the end of the hypural plate.

Body depth—Vertical depth of the body measured at the origin of the pelvic fins (in larvae that have not developed pelvic fins, the midpoint of the body is used).

Origin of anal fin to base of caudal rays—Distance from origin of the anal fin to the end of the hypural plate.

Origin of pelvic fin to base of caudal rays—Distance from origin of the pelvic fin to the end of the hypural plate.

DESCRIPTION OF THE EGGS

Twenty-three eggs ranged from 1.10 to 1.28 mm in diameter (mean = 1.19 mm). The chorion is thin and fragile, unsculptured, and unpigmented. A single oil globule is present, ranging from 0.12 to 0.16 mm in diameter (mean = 0.15 mm). As in most clupeid eggs, the perivitelline space is wide, and the yolk mass is vaguely segmented. For 10 embryos at the blastodisc stage the yolk diameter averaged 59% of the egg diameter, while for 13 advanced embryos the yolk diameter averaged only 53% of the egg diameter. A paired dorsolateral series of tiny melanophores is present on embryos that are about to hatch (Figure 1). *Opisthonema* eggs

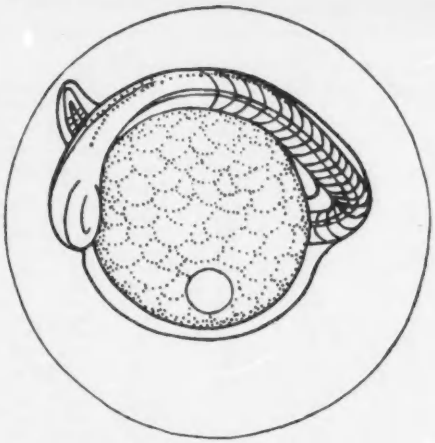

FIGURE 1.—*Opisthonema oglinum* egg.

are similar to those of most other clupeids (e.g., Reintjes, 1962; Simpson and Gonzalez, 1967) but differ markedly in total egg diameter and oil globule diameter from *Harengula* spp., with which they may cooccur. Houde, Richards, and Saksena (1974) reported that the diameter of *Harengula jaguana* eggs was never less than 1.50 mm, and that the oil globule diameter never exceeded 0.10 mm.

MORPHOLOGY OF LARVAE

Meristic values were obtained and these are shown in Table 1. To describe the change in shape and to note changes in various structures, 13 measurements were made. These are shown in Table 2. The larvae are also illustrated for several selected sizes (Figures 2 to 8). *Opisthonema oglinum* larvae, prior to the start of the transition to juveniles, are very slender larvae with a well-developed finfold and long gut. Prior to notochord flexion gut length averages about 86% of the body length. During notochord flexion this increases to 91% because body length is slightly reduced. The abruptness of this flexing is evidenced in the measurement of origin of anal fin to base of caudal rays in Table 2. After notochord flexion this distance is smaller due to the upturning of the notochord. Following flexion (10 mm SL) the gut averages 92% of standard length up until transformation commences at 15 mm SL. At that time there is a gradual shortening of the gut until it becomes about 75% of the standard length as a juvenile. The large finfold decreases at about the time of notochord flexion and is almost lost by the time the anal fin is well differentiated at 13 mm SL, except for a remnant beneath the foregut (Figures 2 to 4).

The first fin to form is the pectoral fin but, as described later under the osteology section, it is not the ossified pectoral fin of the juvenile. The caudal fin, dorsal fin, and anal fin all develop within the finfold itself, and their development is discussed in the osteology section. The pelvic fin is the last fin to be discernible as a small fleshy protuberance at 14 mm SL.

At first, the gut is a straight simple tube. At 5 mm SL it can be differentiated into a foregut and hindgut. The hindgut becomes ridged or banded with tissue, which is quite evident in Figure 4 of a 13.7-mm SL specimen. This ridging is still evident through much of the transitional period (Figure 5).

The most striking feature of development is the anterior migration of the dorsal fin during transformation. The fin nearly has its full complement of rays before this commences and like the shortening of the gut and anterior advancement of the anal fin, it is a rapid change. It is more striking than the latter since the fin is so visible. The predorsal length averages more than 60% of the body length until about 17 mm, then it rapidly decreases to an average of 43% of body length when transformation is completed. The position of both the dorsal and anal fin in relation to the vertebrae also vividly demonstrates this movement (Table 3). The fin movement begins at 15 mm. At that size, the anal fin origin begins to move forward from its position under vertebra 38 (Table 3 and Figure 6) to its final position under vertebrae 33 to 34 at 24 mm (Table 3 and Figure 7). Similarly, the origin of the dorsal fin is transferred forward over vertebra 23 (Table 3 and Figure 6) to over vertebra 15 when larvae measure 19 and 25 mm (Table 3 and Figure 7). To about 20 mm, there are 21 predorsal myomeres and no ossified predorsal bones (free interneurals), but shortly thereafter eight predorsals become ossified.

One character which may be instrumental in separating the various genera and possibly species of clupeids is the distance between the dorsal and anal fins. For practical reasons, the best way to determine this distance is to count

TABLE 1.—Meristic characters of larval and juvenile *Opisthonema oglinum*.

SL (mm)	Caudal rays	Dorsal rays	Anal rays	Pectoral rays	Pelvic rays	Length of last dorsal ray as fraction of prior longest ray	Gillrakers			Scutes		Vertebrae
							Epibranchial	Ceratobranchial	Hypobranchial	Prepelvic	Postpelvic	
3.8-7.4	Nothing countable on 4 specimens in this size range.											
8.4	17	11	—	—	—	—	—	—	—	—	—	—
9.0	18	9	—	—	—	—	—	—	—	—	—	46
9.6	18	9	—	—	—	—	—	—	—	—	—	44
10.0	19	13	—	—	—	—	—	—	—	—	—	—
10.4	19	15	—	—	—	—	—	—	—	—	—	45
10.5	19	—	9+	—	—	—	—	—	—	—	—	—
10.7	19	13	—	—	—	—	—	—	—	—	—	46
12.1	18	15	—	—	—	—	—	—	—	—	—	—
12.5	—	16	7±	—	—	—	—	10	—	—	—	45
13.5	19	17	12	—	—	—	—	—	—	—	—	—
13.7	19	17	16	—	—	0.5X	—	—	—	—	—	—
14.2	19	16	14	—	—	—	—	—	—	—	—	—
14.3	19	14	—	—	—	—	—	8	—	—	—	—
14.3	19	17	10	—	—	—	—	—	—	—	—	46
curved	19	16	16	—	4	—	—	10	—	—	—	—
15.5	19	20	19	—	—	—	—	—	—	—	—	—
15.6	19	20	14	—	5	—	3	13	2	—	—	45
16.2	19	19	19	—	6	0.5X	—	—	—	—	—	—
16.9	19	17	17	—	4	—	—	—	—	—	—	46
17.1	19	19	19	—	5	—	—	10	—	—	—	45
17.2	19	18	18	5	5	—	—	—	—	—	—	45
17.4	19	18	19	—	6	—	—	—	—	—	—	—
17.7	19	19	19	—	6	0.5X	—	—	—	—	—	—
17.7	19	18	16	—	4	—	—	—	—	—	—	—
18.4	19	19	19	—	5	—	3	13	—	—	—	46
19.3	19	19	17	9	6	0.5X	6	12	6	—	—	—
19.7	19	20	21	15	8	0.6X	6	13	4	—	—	45
20.3	19	21	19	13	8	0.7X	8	12	8	8	0	—
21.1	19	20	21	14	8	0.6X	10	17	10	11	2	46
23.4	19	20	22	16	8	0.7X	10	15	9	7	0	—
23.8	19	20	21	15	6	0.7X	11	16	10	12	9	—
24.4	19	20	21	14	8	—	11	16	7	14	2	45
24.8	19	22	23	16	8	0.8X	12	16	11	18	13	—
25.3	19	18	21	16	8	0.7X	10	15	12	13	5	—
25.9	19	20	20	15	8	0.7X	13	16	11	17	13	46
26.2	19	20	21	16	8	0.5X	13	16	13	18	15	46
27.0	—	21	24	16	8	1.3X	16	20	16	18	15	46
27.1	—	20	23	16	—	1.0X	14	18	16	17	14	46
27.1	—	20	23	15	—	1.0X	15	19	15	18	15	46
27.3	—	20	23	16	—	1.1X	15	18	14	18	15	46
28.2	—	20	21	17	—	—	15	18	14	18	15	46
30.0	—	22	22	16	8	1.1X	15	18	14	19	14	—
30.8	19	21	21	17	8	1.2X	18	18	16	17	14	45
34.9	19	22	23	17	8	1.8X	20	22	20	18	16	46
46.8	—	21	21	15	8	2.0X	31	25	32	16	16	—
54.0	19	20	25	16	8	2.5X	34	27	32	18	16	47

the number of myomeres between the end of the dorsal fin to the origin of the anal fin. In *O. oglinum* larvae less than 16 mm, we counted 8, 9, or 10 myomeres between the two fins. Transforming larvae and small juveniles (17 to 25 mm) had from 5 to 7 myomeres between the fins. We were unable to count these numbers with accuracy in specimens longer than 26 mm.

In life the larvae are very transparent and gradually become opaque during transformation because of an increase in pigmentation and a compacting of the visceral cavity. Other than the gross features of the gut mentioned above, the development of the visceral organs was not considered in the present study, but we assume that abrupt changes take place. The swim bladder first appears during transformation. Before transformation, a cavity develops above the anterior end of the hindgut (just posterior to the pelvic fins) in larvae as small as 10 mm, but a definite swim bladder is not apparent until the larvae are 15 mm long. In living larvae the swim bladder is well defined.

OSTEOLOGICAL DEVELOPMENT

Larvae of *O. oglinum* undergo no ossification of any parts before they measure about 10.0 mm SL (all body lengths will be given in standard length unless otherwise indicated). In the youngest cleared and stained larva examined (4.1 mm TL, total length), the cranial bulb was outlined, as were the lower jaw, hyoid apparatus, and dorsal and caudal fin lobes (Figure 2). All these

TABLE 2.—Measurements of larvae and juveniles of *Opisthonema oglinum*. Specimens between dashed lines are undergoing notochord flexion.

Body length	Eye diameter	Snout length	Head length	Length of dorsal fin base	Length of anal fin base	Snout to origin of dorsal fin (predorsal)	Snout to origin of pelvic fin	Snout to origin of anal fin	Origin of dorsal fin to base of caudal rays	Body depth	Origin of anal fin to base of caudal rays	Origin of pelvic fin to base of caudal rays
3.6	0.20	0.10	0.60	—	—	—	—	3.1	—	0.20	0.50	—
4.1	0.18	0.10	0.53	—	—	—	1.9	3.4	—	0.25	0.63	2.0
4.6	0.20	0.10	0.60	—	—	—	2.0	3.9	—	0.20	0.63	2.5
5.2	0.23	0.13	0.73	—	—	—	2.4	4.4	—	0.33	0.63	2.7
7.3	0.25	0.18	0.90	0.35	—	4.8	3.2	6.5	2.2	0.50	0.75	4.1
7.4	0.25	0.18	1.0	0.38	—	5.0	3.3	6.6	2.3	0.60	0.78	4.1
9.1	0.35	0.28	1.1	0.75	—	5.9	4.0	8.1	3.4	0.95	0.95	5.0
9.7	0.35	0.30	1.2	0.85	—	6.5	4.2	8.8	3.3	0.85	0.95	5.4
10.0	0.35	0.27	1.2	0.94	—	6.8	4.4	9.2	3.4	0.95	0.95	5.6
10.1	0.43	0.38	1.5	1.3	—	6.4	4.4	9.4	3.9	1.0	0.63	5.6
10.4	0.38	0.35	1.7	1.5	0.25	6.3	4.6	9.6	3.9	1.1	0.83	5.8
10.7	0.40	0.40	1.7	1.3	0.35	6.7	4.7	9.7	3.9	1.0	1.0	6.0
12.1	0.45	—	—	—	—	7.9	5.2	11.1	—	—	1.0	6.9
12.8	0.50	0.48	2.0	1.7	0.45	8.1	5.8	11.6	4.9	1.1	1.2	7.2
12.9	0.53	0.48	2.1	1.9	0.75	8.2	5.9	11.4	5.2	1.3	1.6	7.2
13.7	0.55	0.73	2.8	1.9	0.63	8.9	6.2	12.4	5.0	1.6	1.4	7.6
14.0	—	—	—	—	—	9.0	6.3	12.6	5.3	—	—	8.0
14.0	0.58	0.63	2.6	2.1	0.60	8.8	5.8	12.9	5.5	1.7	1.4	8.5
15.0	0.63	0.68	2.7	2.1	0.95	9.0	6.7	13.2	6.0	1.6	1.8	8.4
15.8	0.63	0.78	3.0	2.2	0.88	10.0	7.1	13.8	6.3	1.7	1.9	8.8
16.2	0.63	0.60	3.0	2.4	1.0	9.7	7.0	13.9	6.5	1.7	2.1	8.9
16.8	0.80	0.68	3.2	2.6	1.1	10.2	7.7	14.9	6.9	1.9	2.2	9.1
17.1	0.65	0.73	3.1	2.6	1.0	10.0	7.4	15.3	6.9	1.9	2.1	9.5
17.7	0.70	0.75	3.3	2.7	1.2	10.7	8.5	15.3	7.1	2.0	2.4	9.2
17.7	0.80	0.85	—	—	—	10.4	8.1	15.4	—	—	2.3	9.6
18.4	0.83	0.76	3.5	2.9	1.3	10.9	8.8	16.1	7.8	2.5	2.3	9.6
19.3	1.1	—	—	—	—	10.9	9.3	16.3	—	—	3.0	10.0
19.7	1.1	0.85	3.9	3.1	1.8	10.5	9.0	16.6	9.2	2.6	3.1	10.7
20.3	1.2	1.1	4.9	3.5	2.1	10.0	9.8	16.8	10.0	3.3	3.5	10.5
23.4	1.4	1.5	6.0	4.0	3.4	10.7	11.5	18.0	13.1	4.6	5.4	11.9
23.8	1.7	1.6	6.1	4.0	3.7	10.7	12.1	18.1	13.0	4.7	5.7	11.7
24.4	1.5	1.6	6.4	3.7	3.6	12.0	11.9	18.6	12.5	4.4	5.8	12.5
24.8	1.7	1.9	6.7	4.4	4.5	11.0	13.0	18.7	14.0	5.5	6.1	11.8
25.3	1.7	1.7	6.6	4.5	4.2	11.5	12.7	18.9	14.0	4.8	6.4	12.6
26.2	1.5	1.8	6.6	4.0	3.9	12.0	12.6	19.7	14.2	4.8	6.5	13.6
27.0	1.9	1.6	6.4	4.3	4.3	12.3	13.5	19.7	14.7	5.7	7.3	13.5
27.1	1.8	1.9	7.3	4.4	4.4	11.6	14.2	20.2	15.5	5.8	6.9	12.9
27.1	1.9	1.7	6.7	4.0	4.0	11.4	13.3	20.3	15.8	4.5	6.8	13.8
27.3	1.6	1.8	6.8	4.1	4.3	11.8	14.0	19.9	15.5	5.0	7.0	13.3
28.2	1.9	1.9	7.3	4.3	4.2	12.5	14.3	20.7	16.7	5.0	7.0	13.9
30.0	2.3	2.4	8.5	5.0	5.0	13.0	15.5	22.8	16.8	8.3	8.2	14.5
30.8	2.2	2.4	8.0	5.0	5.0	13.4	15.7	22.9	17.3	7.7	7.9	15.1

structures were clear, however, indicating no ossification. The first structures to ossify were the dentaries and maxillaries when specimens measured about 10.0 mm (bone nomenclature follows Mead and Bradbury, 1963). Almost simultaneously, the very thin cleithral ring (cleithrum, supra-cleithrum, and postcleithrum) and the hypurals began to ossify very slightly. At sizes between 12 and 13 mm, the skull bones began to ossify, as did the vertebral rings. As size increased, various other parts of the fish began to ossify—the caudal fin rays, parts of the branchial apparatus (ceratobranchials, hypobranchials, epibranchials), and the dorsal and anal fin rays; skull bones ossified further (Figure 3). At about 20 to 22 mm, essentially all bony structures of the larvae had at least begun to ossify, and some were well developed.

Vertebral development

No ossification took place before 10 mm, but cartilaginous structures were visible. At the time of notochord flexion, seven hypural elements were formed (four superior and three inferior elements including the parhypural). In specimens measuring 10.5 mm, the hypurals were weakly ossified but the seven elements were distinct. The first vertebral centra to ossify was the first preural centrum and the ventral portion of the centra of the first and second ural centra. This differs somewhat from the development noted in

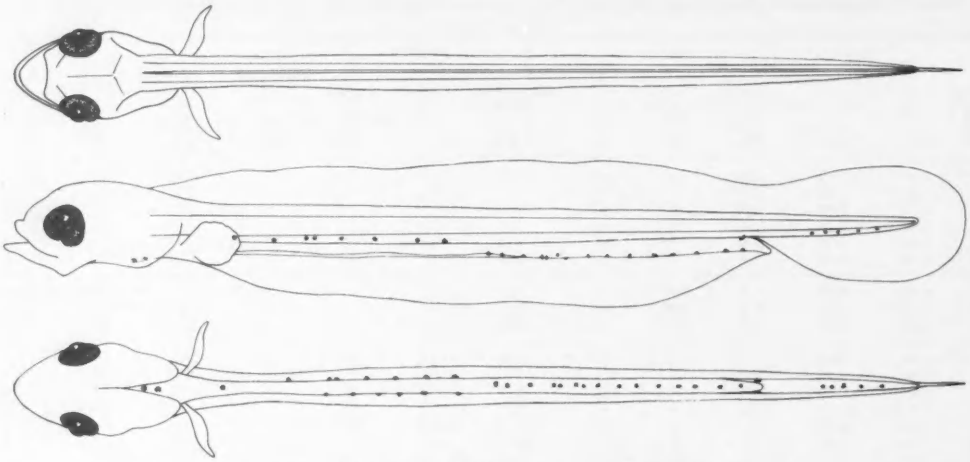

FIGURE 2.—*Opisthonema oglinum* larva 4.0 mm total length.

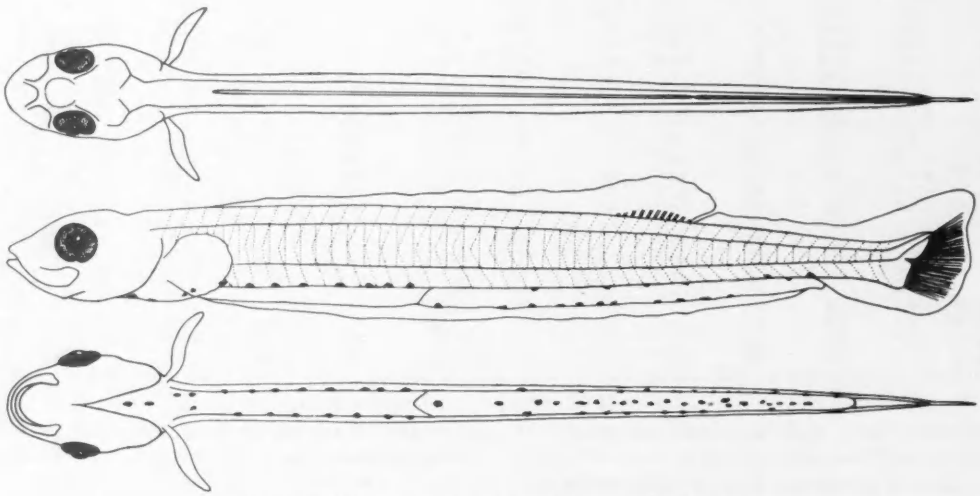

FIGURE 3.—*Opisthonema oglinum* larva 10.7 mm standard length.

H. jaguana by Houde et al. (1974). They noted that the second ural vertebra ossified first. Epural development displayed some variation (two instead of the normal three in some specimens), as was also noted in *Harengula* by Houde et al. (1974). Hollister (1936) noted this variation in *Harengula* but not in *Opisthonema*. Other than these differences, caudal development was essentially the same for *Opisthonema* and *Harengula*. For a more complete account, consult Houde et al. (1974).

At 10.5 mm, ossification also started on vertebrae 12 through 40. This ossification starts on the dorsal and ventral surfaces of the centra, thus making it quite easy to count vertebrae. The degree of ossification of these vertebrae indicates that the middle ones were most ossified, with ossification proceeding anteriorly and posteriorly. By 12.5 mm, dorsal and ventral ossification of the centra is complete on vertebrae 2 through 41, while only the ventral centrum surface has ossified on the first vertebra and the

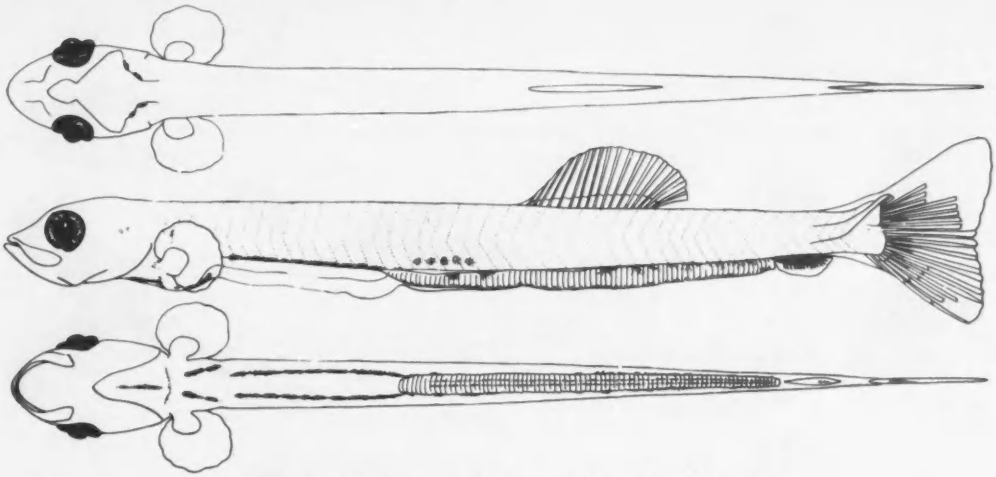

FIGURE 4.—*Opisthonema oglinum* larva 13.7 mm standard length.

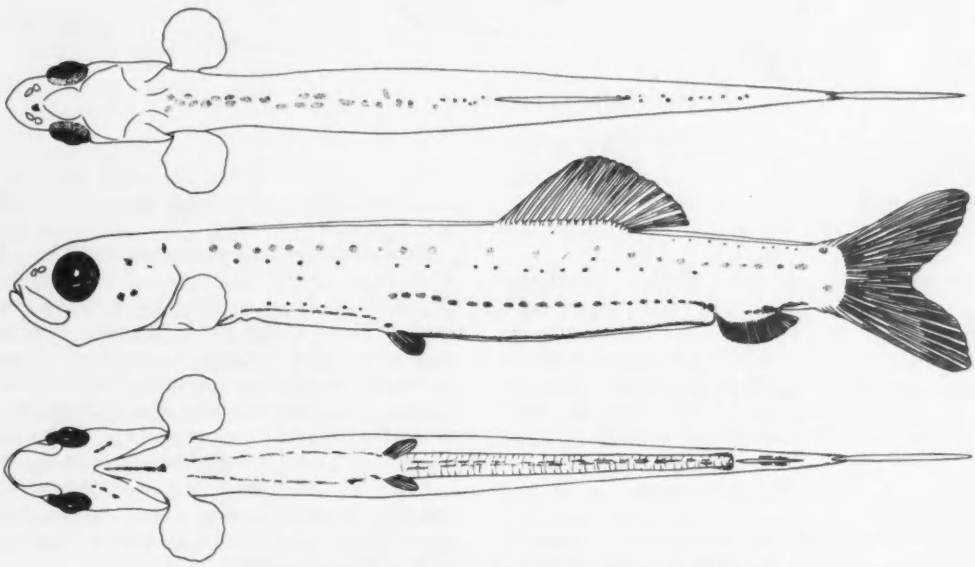

FIGURE 5.—*Opisthonema oglinum* larva 17.1 mm standard length.

three preceding the ural centra. These three centra immediately anterior to the first preural were wider ventrally and had large spaces between the vertebral segments. At 15.5 mm, all vertebral centra were partially ossified and evenly spaced with narrow spaces between. In the first preural and ural centra, the three rings of ossification had widened, but the middle ring was still wider ventrally than dorsally. (This asymmetrical shape of the ossified rings of the vertebrae associated with the caudal region obviously corresponds to flexion of the notochord. The ventral surface is longer after flexion than the dorsal surface and, consequently, to keep the

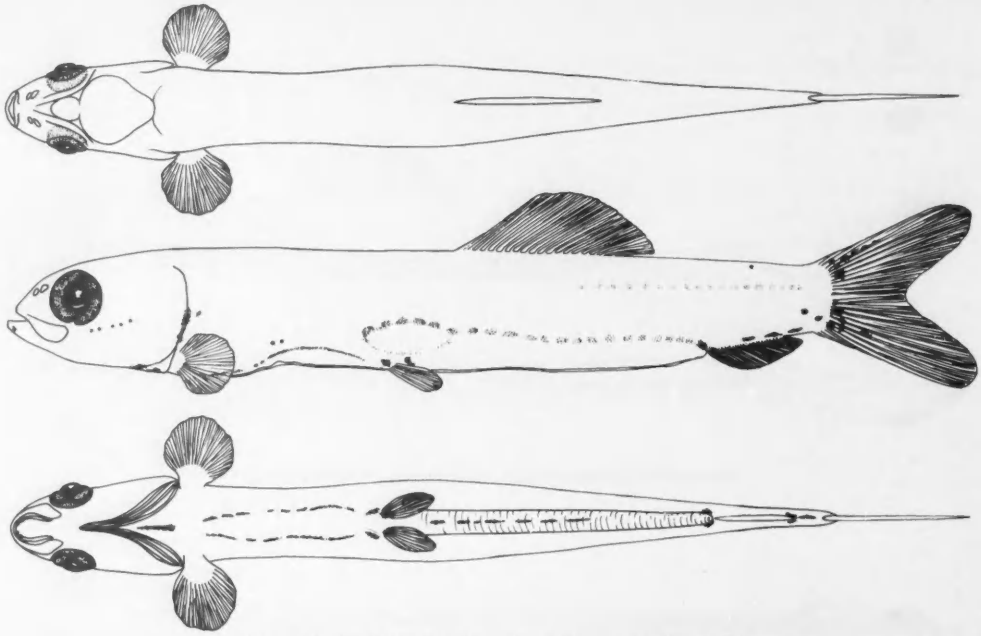

FIGURE 6.—*Opisthonema oglinum* larva 19.7 mm standard length.

spaces between ossified segments equal, the segments ossify in a wedgelike shape.) By 17.1 mm, the three rings had widened appreciably and the spaces had narrowed.

Neural and hemal spines ossify in a posterior to anterior direction. Neural spines are well formed over the last three centra, which precede the first preural well before ossification on the centra is completed. By 17.1 mm, ossification of these elements is just complete to below the dorsal fin, and by 22 mm they are all ossified.

Fin Development

The earliest fin development was of the caudal and dorsal fins, more-or-less as lobes, at about 4 mm TL. This early development may be due to a rearing abnormality since fin development is seldom seen in field-caught larvae less than 7 mm SL. Increasing numbers of caudal and dorsal rays were defined at lengths from 6 to 8.4 mm, but were not clear enough to count until our 8.4-mm specimen (17 caudal and 11 dorsal rays, Table 1 and Figure 3). Between 8.4 and 10.0 mm, the final two caudal rays were differentiated to complete the adult complement of 19 principal cartilaginous rays (10 superior and 9 inferior).

Rays continued to be added to the dorsal fin: 16 were present at 12.5 mm and 18 to 20 were present from 15 to 20 mm (Table 1, Figures 4 through 7). As growth proceeded, one or two more rays were added to complete the adult complement of 21 or 22 dorsal rays (Figure 8). In adult *Opisthonema*, the last ray of the dorsal fin is elongate—more than twice as long as the next longest ray. Until about larval size of 20 mm, the last ray was half as long as the longest ray, but from then on it began to elongate. From about 27 mm, the last ray grew longer than the prior longest ray (Table 1).

The anal fin formed later than the dorsal, from a thickening of the ventral finfold in the relatively short space between the anus and the caudal fin (Figure 3). At 10.5 mm, the fin rays had begun to differentiate and nine rays could be counted. Ossified rays increased rapidly to 14, 15, or 16 at about 14 mm, after which rays were added more slowly to sizes from 15 to 20 mm. Between 14 and 20 mm, counts of 17 to 20 rays

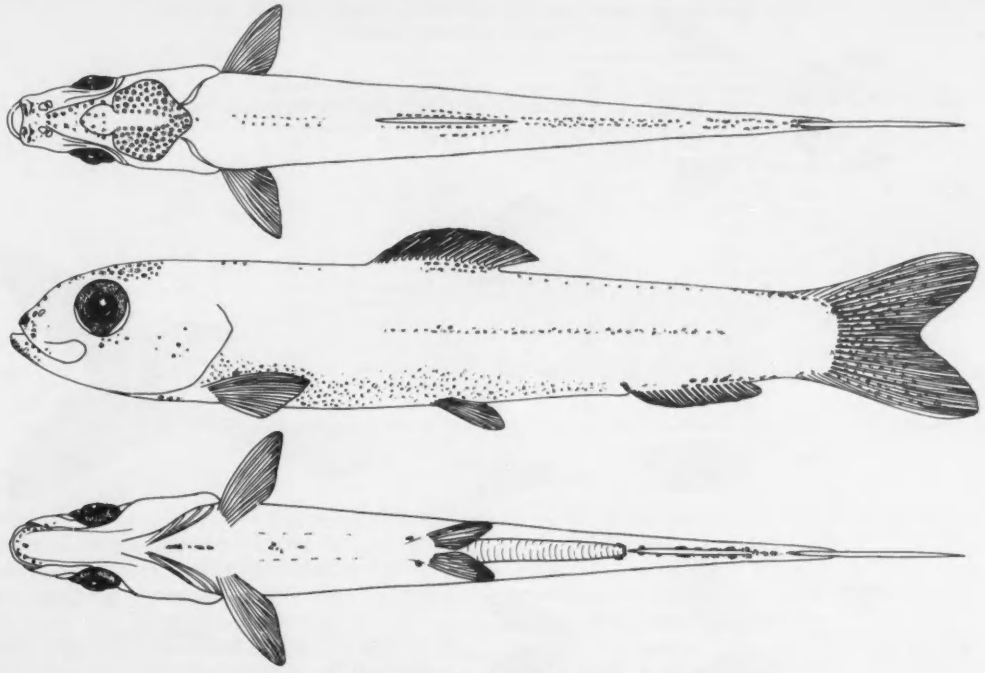

FIGURE 7.—*Opisthonema oglinum* juvenile 24.4 mm standard length.

were produced (Figure 7). Only about three or four more rays were added, from 20 mm, until the adult complement of 21 to 25 anal rays was reached at 30 mm and over (Table 1, Figure 8).

The pectoral fin appeared as a small, fan-shaped structure just behind the cleithral ring, but this structure enlarged gradually (Figures 2 to 7). [Within the fan, "ray areas" differentiated soon thereafter, but these had no apparent relation to where rays actually ossify.] Ossified rays first appeared at about 17 mm (five rays; see Table 1) and quickly increased to about 10 rays at 19 mm. The rounded fan shape of the pectoral fin changed into the pointed shape characteristic of adults between 19 and 23 mm (Figure 7). At 21 mm, specimens had about 13 or 14 rays, and the adult complement of 15 to 17 rays was reached at 23 to 25 mm. The sequence of ray ossification was in a dorsal (uppermost) to ventral (lowermost) direction.

Ossified pelvic rays appeared earlier than the pectoral rays. At about 13 mm, larvae had about four rays (Table 1), and at about 15 mm they had five or six (Figure 5). The number of rays seemed to remain static for about the next 5 mm of growth (10 specimens in the 15 to 20 mm size range), but rather suddenly two more rays appeared at about 20 mm (Table 1, Figure 7). The pelvic ray count held constant, though size increased to 50 mm, but in adults a ninth ray is added as a flattened, segmented ray closely adnate to the second (formerly most lateral) ray to produce nine total rays. In our larger (30 to 54 mm) specimens (Figure 8) the flattened first ray does not appear to be present. If it is, the ray is so tightly attached to the second ray that the two seem to be a single unit.

Cephalic Development

No ossification of any bones appeared before specimens reached about 10.0 mm. In larvae as small as 4.1 mm TL, the cranial bulb, dentaries, and hyoid bones were visible as cartilaginous elements. At about 10.0 mm, the maxillaries and dentaries were easily distinguished and began to show slight ossification (by stain uptake). The jawbones more-or-less steadily increased in

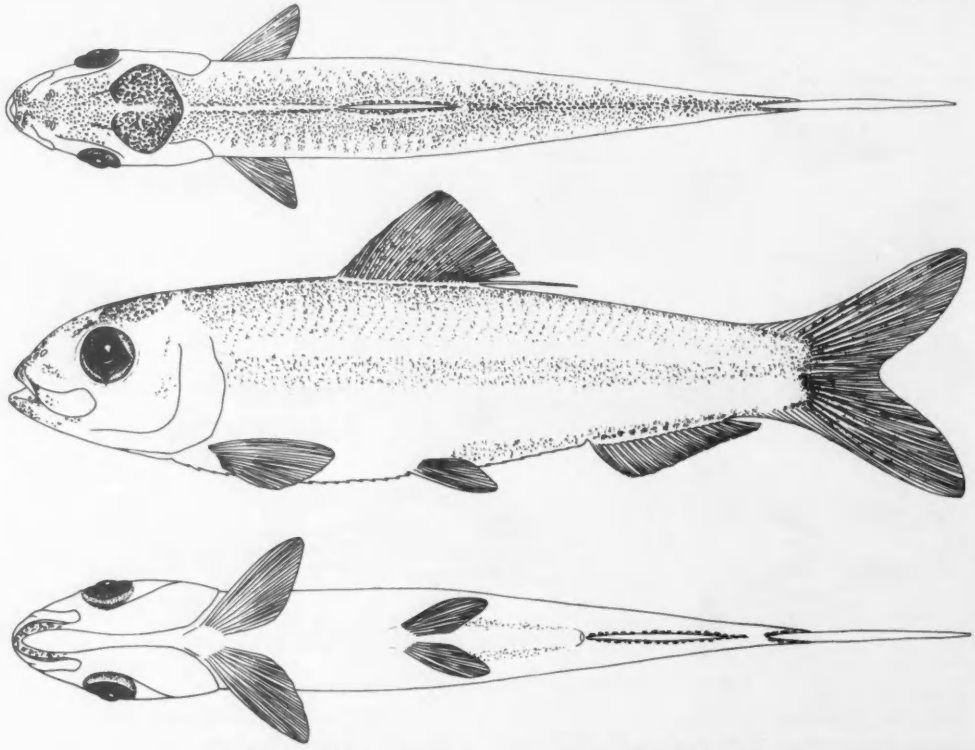

FIGURE 8.—*Opisthonema oglinum* juvenile 30.8 mm standard length.

size and became more heavily ossified; at about 14 mm, small teeth were found on the ventral edge of the maxillaries and the anterodorsal edge of the dentaries. Concommitantly, the hyoid apparatus continued to develop steadily, particularly the ceratohyals and hypohyals, which were quite distinct and slightly ossified by 14 mm. By about 17 mm, the two supramaxillaries were differentiated and partly ossified but had not obtained their characteristic adult shapes. The premaxillaries also were partly formed and ossified as two distinctly separate units close to the anterior tips of the maxillaries. By 19 mm, the articular was well developed but not fully ossified. The posterior supramaxillary was almost completely ossified but not the anterior supramaxillary. Maxillaries maintained an ossified posterior edge (the region of growth), and the teeth on the ventral edges were still prominent. The ceratohyals and urohyal were more ossified, and two small centers of heavy ossification were present in the hypohyals. One structure of interest was the presence of teeth on a few specimens on the basihyal. In a 12.0-mm specimen, two large erect teeth were noted; a 15.6-mm specimen had one such tooth, which was also present on a 17.1-mm specimen. No such teeth were evident on a 25.9-mm specimen, indicating that these teeth may be variable and limited in occurrence. Houde et al. (1974) noted the presence of these temporary teeth in *Harengula*. The branchiostegals ossified in the following sequence: fourth branchiostegal slightly ossified at 15.5 mm; fourth well ossified at 17.1 mm; fourth, third, and second ossified; first visible as cartilage; fifth and sixth not visible at 19.7 mm. By the time specimens reached 24 mm, six well-ossified branchiostegals were present, the supramaxillaries were ossified but the posterior supramaxillary had not reached a complete adult shape, all the hyals were partly ossified, the well-developed premaxillaries were ossified and

TABLE 3.—Position of dorsal and anal fins during the transformation period in larvae of *Opisthonema oglinum*.

SL (mm)	Dorsal origin over vertebra	2d dorsal pterygiophore opposite neural arch	Anal origin under vertebra	1st anal pterygiophore opposite haemal arch
15.5	25	21	38	36
17.1	23	—	37	35
17.2	22-23	20	38-39	36
18.4	23	20	38	35-36
19.7	20	17	36	34
21.1	16	12	—	—
24.4	16	11	33	30
25.9	15-16	11	33	30
26.2	16	11	33-34	30
27.0	14	9	32	29
27.1	15	11	33	30
27.1	15	10	33	30
27.3	14	10	33	30
28.2	15	10	33	30
30.8	15-16	10	33	30
34.9	15	10	34	30
54.0	15	9	34	30

joined at the anterior tip of the upper jaw, and the maxillaries appeared to be fully formed.

At about 10 mm, the cleithral ring was obvious as a thin ring of ossified bone almost encircling the head and forming a posterior line of demarkation. The three bones that actually form this ring are the supracleithrum, cleithrum, and postcleithrum, which developed fairly uniformly to about the time the pectoral fin began to develop ossified rays (about 15 to 17 mm). Thereafter, the cleithrum became the dominant element.

A cartilaginous cranial bulb was visible in our smallest larvae, but no elements were differentiated or ossified until about 12 mm. At that size, bone elements (e.g., the sphenotics, parietals, epiotics, and pterotics) were slightly outlined. Between 12 and 13 mm, the vomer and parasphenoid began to show considerable ossification, and the pterotic and prootic bullae were differentiated by ossification of the surrounding bones. The frontals began to form when specimens measured about 15 mm, and about 19 mm they were partly ossified (but not fully formed), and sensory canals were present within the bones. Canals also formed at the 19-mm size in the prootics and sphenotics, and the prootic bulla was the most obvious structure in the skull because of the heavily ossified bone around it.

The quadrate and the pterygoids had begun to form by 19 mm, and the articular had increased in size but was not yet fully ossified. At about 21 mm, the nasals began to form as thin, small plates at the anterior ends of the frontals. Formation of supraorbitals had also begun, the anterior one being moderately well developed and quite separate from the posterior one. At the 21-mm size, it also appeared that most of the head bones were at least partly formed, and ossification ranged from slight to considerable. By 25 mm, the prootic bulla was well encased in heavy bone, the sclerotics had begun to ossify along with the supraorbitals, the ethmoids had begun to form and ossify at the anterior ends of the frontals and just behind and above the premaxillaries, the vomer was quite large and well ossified, most sensory canals were partly to fully formed and encased in bone, the postorbitals had begun to form, and the pterotic bulla (which lagged far behind the prootic in development) began to grow larger. From 25 mm through the juvenile period, growth of the skull bones was restricted primarily to an increase in size and consolidation within the several multibone complexes; the dorsal and lateral frontoparietal foramina decreased in size as the bones increased, and the characteristic striae of the dorsal surface of the frontoparietals began to form; the pterotic bulla finally became larger than the prootic by about 34 mm; and the palatines began to ossify. During the 30- to 50-mm range, most of the cranial structures assumed their adult configuration, the dorsal frontoparietal foramina completely closed up, and the lateral foramina became reduced in relative size.

The elements of the opercular complex—primarily the opercle and preopercle—began to differentiate at about 15 mm. Shortly thereafter the subopercle and interopercle began to form and by 21 mm most of the opercular series appeared to be about halfway ossified; the interopercle seemed to be the most weakly ossified. By 25 to 26 mm, the interopercle had grown to articulate with the quadrate and angular and the hyals. The other opercular bones had become quite well developed, but the posteroventral edges remained unossified, evidently to permit continuous growth.

Branchial Development

The ceratobranchials were the first elements to develop in the branchial system, becoming evident at about 10 mm. By about 12 to 13 mm, the ceratobranchials showed a slight uptake of stain, indicating that they had begun to ossify. At 14 mm, the hypobranchials had begun to differentiate, and a few unossified rakers were visible on the ceratobranchials.

The ceratobranchials, the first, second, and third epibranchials, and the hypobranchials all developed as more-or-less straight rods (although the epibranchials also developed small dorsal extensions for attachment of suspensory ligaments). The first rakers appeared on the ceratobranchials at about 12 mm (Table 1) and held almost constant between 10 to 13 rakers to about 17 mm. Two or three rakers appeared on the epibranchials and hypobranchials when larvae reached about 15 mm. The numbers of rakers on all three elements gradually increased with the numbers on the epibranchials and hypobranchials almost equal but from two to four lower than on the ceratobranchials, up to about 30 mm (Table 1). At the 30-mm size, all three bones had an equal number of rakers, but beyond that size the ceratobranchials seemed to lag behind the epibranchials and hypobranchials by five or six rakers. In adults, the hypobranchials and ceratobranchials are almost equal in numbers of rakers (30 to 45), producing lower branch counts of 60 to 90, but the epibranchial rakers almost equal the combined lower branch counts.

The fourth epibranchial (E4) was the first to develop a slight vertical extension when specimens measured about 14 mm; the shape of the fourth epibranchial at this stage is more-or-less like an inverted "T"—the crossbar (the basal shaft) is ventral and the vertical segment extends dorsally from it. On the dorsal and posterior edges a developing cartilaginous capsule (see Miller, 1969; Figure 2, for the adult configuration of the capsule) is fused to the developing E4 bone; this capsule is also joined to the epiceratobranchial "elbow." A vertical slit is present in the posterior side of the capsule, and the two raker series that will eventually grow throughout the length of the lumen of the epibranchial organ begin growing along the sides of the posterior slit. Dual fourth epibranchial raker series are present, with the lateral series growing along the ventrolateral edge of the fourth epibranchial bone, outside the epibranchial organ, and the medial fourth epibranchial series is enclosed in the organ along the anterolateral edge of the slit in the cartilaginous capsule. The single fifth epibranchial series grows along the posteromedial edge of the slit. By 15.5 mm, the vertical extension on E4 had grown much heavier and the characteristic posterior foramen had formed (see Miller, 1969; Figures 2 and 4). Three raker tubercles were present along the edges of the posterior slit (which had just begun to form). By 17 mm, the cartilaginous capsule had begun to increase in size, and by 19 mm there were four or five raker tubercles in the posterior slit. Almost no ossification had yet appeared on the fourth epibranchial, and the posterior foramen was quite large. Ossification began at about 20 mm, and by about 25 mm the posterior end of the basal shaft had expanded vertically (it resembled an axe blade), and the vertical shaft had also broadened and ossified quite heavily. At this stage there were about eight rakers along the edges of the posterior slit. When larvae measured 26 mm, the lumen of the organ had begun to form; it extended anterodorsally within the cartilaginous capsule from the bridge of the posterior slit, and 10 rakers appeared along each edge. One or two rakers were present in the developing lumen. By 30 mm, the lumen had elongated to about one-third of a full loop [the epibranchial organ in *Opisthonema* is the continuous-tube type (see Bertmar, Kapoor, and Miller, 1969; Miller, 1969) in which the lumen and included rakers extend for a full loop in adults] and there were about 15 to 20 rakers in the lumen. By 35 mm, the lumen was about a half of a full loop and

had curved anteriorly beyond the width of the vertical shaft of E4. About 30 rakers were present in each series at this stage and the epibranchial organ and E4 bone were assuming adult configuration. Estimates made on adult specimens indicate that in a full-loop, continuous-tube epibranchial organ, the definitive number of rakers in the included medial E4 and single E5 series each at least equal the total of rakers on the whole first gill arch. There are about 120 rakers in adults 100 mm or longer (Berry and Barrett, 1963). We may therefore infer that the number of rakers in the epibranchial organ increases gradually with increasing size of the fish, to about 120 or more in each series.

PIGMENTATION

Melanophores were present along the ventral midline in the smallest specimens studied (4 mm) —one or two melanophores beneath the heart just anterior to the pectoral symphysis, and a paired row along the base of the hindgut (that portion of the gut posterior to the site of the pelvic fins) continuing to the anus, and a row on the ventral midline posterior to the anus. A dorsolateral row of melanophores occurred on each side of the foregut (that portion of the gut anterior to the pelvic fin region). The eye was pigmented but no other melanophores were present (Figure 2). By 10 mm, the posterior ventral row was distributed along the posterior edge of the hypural bones, and a few internally placed melanophores appeared dorsolaterally on each side of the hindgut. The remaining melanophore pattern was basically unchanged (Figure 3). By 15 mm, the melanophores had developed into streaks of pigment along the base of the isthmus, dorsolaterally along the anterior gut, along the base of the posterior gut, and on each side of the base of the anal fin. Internal melanophores above the posterior gut had taken on a well-defined, broken-lined pattern and had begun to advance anteriorly, particularly forming a slight arch in the area of the swim bladder (Figure 4). Melanophores appeared on the cleithrum near the hindbrain, and the hypural melanophores at first clustered on the bases of the lower lobe of the caudal fin but, by 17 mm, melanophores appeared on both lobes of the caudal fin. Between 15 and 24 mm (transformation period), melanophores varied somewhat in time of appearance. In some specimens a melanophore appeared medial to the left nostril (Figure 5, dorsal view). Melanophores appeared both dorsally and ventrally on the swim bladder as it developed (Figure 6). During this period melanophores also began to appear on the dorsum, first posterior to the dorsal fin, then anteriorly. Melanophores also appeared along the lateral midline and over the hypural bones internally. The internal pigment associated with the vertebral column of these larvae is quite pronounced, particularly during transformation. A few internal melanophores over the posterior centra were first noted in a cleared and stained 12.1-mm specimen. By 15 mm, one or two melanophores or groups of melanophores were noted above each vertebra. The melanophores over the anterior vertebrae are lost or reduced by 19 mm. Some individual variation, however, is evident in both the internal and external pigmentation. The dorsal external pigmentation is noticeably reduced in the 19.7-mm specimen (Figure 6) as compared to the 17.1-mm specimen (Figure 5). The expanded state of most melanophores (a probable result of rearing under continuous illumination) makes detailed counts of melanophore patches quite difficult. Following transformation, melanophores were visible over the brain and on the jaws as well as in increasing quantities on the dorsum, lateral midline, over the gut, and in the caudal fin rays (Figure 7). By 30 mm, the dorsal pigment had increased, the foregut pigment was lost, and melanophores were seen in the dorsal fin—essentially the adult pattern (Figure 8).

In life, the larvae are transparent and the only noticeable features are the heavily pigmented eyes. The gut is usually noticeable because of the food contained in it. In larger larvae, the swim bladder is decidedly noticeable as a bubble above the gut (Figure 6). Melanophores are invisible until the specimen is examined under magnification.

ACKNOWLEDGMENT

Elbert H. Ahlstrom (Southeast Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, Calif.) and Peter J. Whitehead [British Museum (Natural History)] reviewed the manuscript and their helpful comments and criticism are greatly appreciated.

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THE INFLUENCE OF TEMPERATURE ON LARVAL AND JUVENILE GROWTH IN THREE SPECIES OF SOUTHERN CALIFORNIA ABALONES[1]

DAVID L. LEIGHTON[2]

ABSTRACT

Larvae of the abalones *Haliotis rufescens*, *H. corrugata*, and *H. fulgens* displayed most rapid growth and best survival at 15°-18°, 18°-21°, and 20°-23°C, respectively. Survival of larvae and postlarvae was poor above these optimal ranges. However, juveniles 3 mo to 1 yr old were tolerant of a broader temperature range. The warm-water species, *H. fulgens*, increased in shell length at an average rate of 88 μ per day at 26°C. Mean shell elongation rates were 77 and 64 μ per day in *H. rufescens* and in *H. corrugata* at their respective optima.

An expanding body of literature exists concerning aspects of the biology and culture of the abalone *Haliotis* (e.g., Sakai, 1962; Oba, 1964; Tamura, 1966; Imai, 1967; Tanaka, 1969; Shibui, 1971a; and McBeth, 1972, which succeeded the pioneering studies of Murayama, 1935, and Ino, 1952). In these studies little attention was directed to problems of larval development, and essentially no information has been obtained on the limitations imposed by temperature on growth and survival of larvae and postlarvae with the single exception of the observations on *H. sorenseni*, reported by Leighton (1972). In 1962, Kan-no and Kikuchi related results of a 3-wk experiment in which juvenile *H. discus hannai* were reared at five different temperatures, but most investigators have merely reported the range of temperature prevailing during observations (e.g., Oba, 1964; Shibui, 1971b).

This paper describes results of experiments in which groups of larvae, postlarvae, and juveniles were reared at a series of temperatures encompassing the natural range to examine the influence of these factors on development and survival. Larvae were obtained from three American west coast species spawned in the laboratory: The red abalone, *H. rufescens*, the pink abalone, *H. corrugata*, and the green abalone, *H. fulgens*.

MATERIAL AND METHODS

Ripe abalone were collected off southern California by diving. In transportation to the laboratory, care was taken to avoid subjecting the animals to desiccation or other physical shock which might have induced premature release of gametes. Adult abalone were allowed a laboratory "conditioning period" of about 2 wk before attempts were made to induce spawning. Water temperature in tanks containing abalone of both sexes was raised approximately 5°-8°C above ambient, following the thermal shock method of Ino (1952) and Oba (1964); a procedure which was only occasionally successful. Most productive spawnings in terms of quantity and viability were those which occurred spontaneously in the laboratory. Natural cues and events associated with "mass spawnings" are not well understood (Owen and Meyer, in press) and were not investigated in this study.

Fertilized eggs were collected as soon as possible after their release. The eggs, which settle rather rapidly, were siphoned or pipetted into freshly filtered seawater (Cuno filter unit,[3] ca. 5 μ) at the same temperature as that of the spawning environment. Repetition of the process several times, each time using freshly filtered seawater, was usually sufficient to wash eggs free of excess sperm and debris. Incubation was carried out at ambient temperatures and larvae treated as described elsewhere (Leighton, 1972).

While some experiments were performed with eggs at early cleavage stages, most observations

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[2]Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92037; present address: California Marine Associates, P.O. Box 136, Cayucos, CA 93430.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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were initiated with newly hatched trochophore larvae. Trochophores normally hatched from eggs at 15°-18°C within 12 to 18 h. Shortly after hatching, larvae swim to the surface (negative geotaxis) and are easily drawn into a pipette for transfer to experimental containers.

Thermal influence on development and survival of larvae and postlarvae was observed using a temperature gradient apparatus; an aluminum block (30 × 15 × 150 cm) bored to accommodate replicate series of test tubes (25 ml). Cooling coils and heating elements at opposite ends maintained a temperature differential (range: 7°-31°C) with but slight fluctuation (±0.5°C per gradient position) over the course of the average experiment (2-4 wk). The apparatus is similar to that used with *H. sorenseni* larvae (Leighton, 1972) and has been thoroughly described elsewhere (Thomas, Scotten, and Bradshaw, 1963).

In the typical experiment duplicate series of 10 tubes, each tube containing 20 ml of seawater, were placed in the thermal gradient with 50 eggs or larvae. Incubation was carried out in darkness. A foam urethane cover insulated the apparatus. Inspection of the tubes was made daily during the first week and on alternate days thereafter to determine the stage of development attained. As abalone larvae are lecithotrophic, feeding was not necessary until settlement. At that time a mixture of three species of pennate diatoms (*Nitzschia* spp.) was supplied.

Studies on postlarvae were also conducted using the temperature gradient block. Between two and five individuals were placed in each tube. Postlarvae 1-2 mo of age were picked individually from walls of culture containers (Pyrex beakers or polyethylene pails) using a finely bevelled applicator stick. Several drops of the diatom culture were added to each tube twice weekly over the usual 2-wk observation period.

To examine the effect of temperature on the success of juveniles, groups of 8-12 individuals were reared in six 10-liter polyethylene containers maintained at 12°, 15°, 18°, 21°, 24°, and 27°C (±1.0°). Water was continuously aerated and the entire volume exchanged once a week. Food was either a mixture of unicellular and filamentous algae cultured within each container under illumination of a fluorescent lamp or fronds of the brown alga, *Egregia laevigata*, collected in fresh condition every 3-4 days. Growth of juvenile abalones was measured for month-long intervals in these experiments.

Progeny of each spawning were maintained in the laboratory for over 1 yr providing comparative information on juvenile growth rate in aquaria. Diatoms and minute filamentous algae served as food during their first few months. Older juveniles were provided larger algae, *Egregia laevigata*, *Eisenia arborea*, *Macrocystis pyrifera*, and *Laminaria farlowii*.

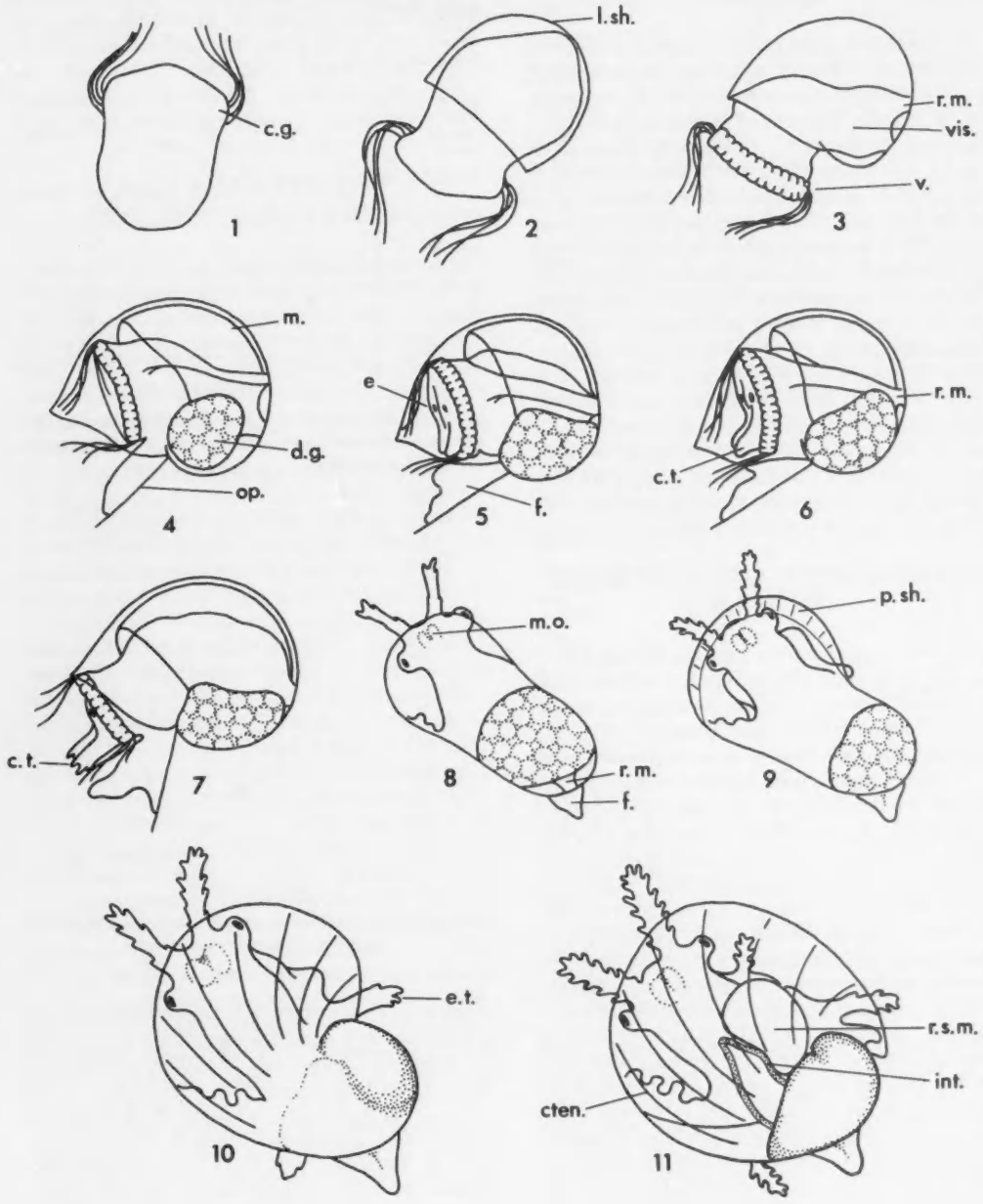
DEVELOPMENTAL FEATURES OF LARVAE, POSTLARVAE, AND JUVENILES

While morphogenesis is gradual and does not progress in a stepwise manner, various stages of larval and postlarval development are recognizable. Development rate was measured in terms of the time required for larvae to first gain features distinctive to each stage. Eleven such stages are passed from trochophore larva to circular-shelled postlarva (Figure 1). Settlement (the crawling stage) marks the end of larval life. Postlarval development then begins with the deposition of peristomial shell and persists to formation of the first respiratory pore ("notch stage," Leighton, 1972) at an age of 1-3 mo. Thenceforth to first sexual maturity the abalone may be regarded as juvenile.

FIGURE 1.—1) Trochophore larva after hatching. 2) Cap-shell early veliger larva. 3) Inflate-shell veliger (torsion stage). 4) Early operculate veliger (preeye spot). 5) Incipient cephalic tentacle stage operculate veliger. 6) Midformed cephalic tentacle stage. 7) Digitate or branched cephalic tentacle stage. 8) Crawling and settling stage. 9) Peristomial shell stage postlarva. 10) Midasymmetric shell postlarva. 11) Circular-shell postlarva.

Labelled structures:

c.g.,	ciliated girdle
c.t.,	cephalic tentacle
cten.,	ctenidium
d.g.,	digestive gland
e.,	eye spot
e.t.,	epipodial tentacle
f.,	foot
int.,	intestine
l. sh.,	larval shell
m.,	mantle
m.o.,	mouth with odontophore
op.,	operculum
p.s.,	peristomial shell
r.m.,	retractor muscle
r.s.m.,	right shell muscle
v.,	velum
vis.,	viscera


c.g.
1
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r.s.m.
int.
cten.
11

RESULTS

In the course of the study six batches of larvae were obtained from *Haliotis rufescens*, while three productive spawnings occurred with *H. corrugata* and *H. fulgens*. Year-round spawning in *H. rufescens* was predicted by Boolootian, Farmanfarmaian, and Giese (1962) and Young and DeMartini (1970) from field sampling for gonad indices. I found spawning adults every month of the year (1969-71) in samples taken from Estero Bay (central California) and in the present study with *H. rufescens* from southern California, laboratory spawnings were obtained in January, February, April, September, November, and December. *Haliotis corrugata* and *H. fulgens* spawned only during the months of April, June, and October. Members of the shallowwater species, *H. cracherodii*, held in the laboratory for another study, spawned in early spring and early fall. *Haliotis sorenseni* produced viable gametes only during late winter (Leighton, 1972).

DEVELOPMENT AND HATCHING IN EGGS

At 14°-16°C (ambient for La Jolla during most of the year) eggs of all species hatched within 18-24 h. Generally, development to hatching appeared normal over a rather broad thermal range. At hatching, however, consequences of inappropriate incubation temperatures became pronounced as trochophore larvae at and near thermal limits became highly abnormal in appearance and behavior and usually succumbed within 48 h, particularly at higher temperatures. Bizarre ciliated bodies predominated at high extremes of temperature while retardation and paralysis occurred at lowest temperatures. Commonly torsion was incomplete in larvae held at subnormal temperatures. A consequence of ensuing abnormality and mortality near thermal limits is apparent in the series of curves generated for development during the first several days of larval life. Attrition at upper and lower extremes and relatively high survival and rapid growth at optimal temperatures is reflected in the sharply peaked curves for larval development rate versus temperature. In *H. rufescens*, for example, eggs developed in an apparently normal manner over the range 10°-23°C, but larval growth after hatching became restricted to the comparatively narrow range 13.5°-20.0°C (Figure 2). The apparent shift of the peaks of curves with time to suggest true optima at temperatures about 2°C lower than observed in trochophore larvae was found in all species studied due to supraoptimum mortality.

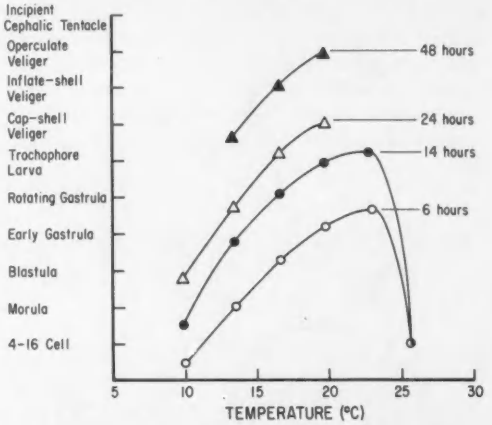

FIGURE 2.—Development of eggs of *Haliotis rufescens* held at different temperatures over a period of 48 h. Mortality occurred above 20°C after 14 h.

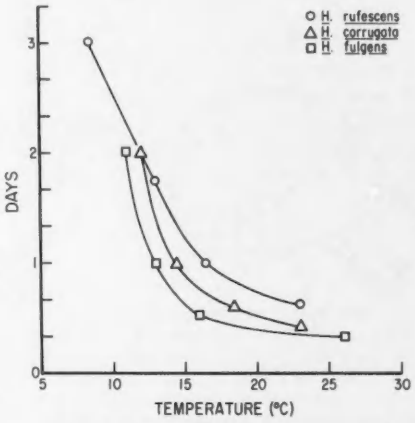

FIGURE 3.—Hatching time for eggs of three species of *Haliotis* incubated at several temperatures.

Hatching time was strongly dependent on temperature and ranged between 10 and 72 h. Both *H. corrugata* and *H. fulgens*, at temperatures supporting rapid but normal growth (their respective thermal optima), reached the point of hatching sooner than did *H. rufescens* (Figure 3). Strongest contrast in specific development rate is seen in the stage attained at supraoptimum temperatures (2°-3°C above optimum). In 2 days: *H.*

rufescens (near 19°C) reached the early (preeye spot) operculate stage, *H. corrugata* (near 23°C) had formed eyespots and cephalic tentacle buds, and *H. fulgens* (near 25°C) had become mid-cephalic tentacle operculates. In the latter, settling was observed as early as 3 days after fertilization.

OBSERVATIONS ON TROCHOPHORE LARVAE

When swimming trochophore larvae rather than developing eggs were introduced to the thermal gradient system, survival was improved. In experiments initiated with fertilized eggs, survival beyond 3 days in the 20-ml tubes was low despite routine addition of dihydrostreptomycin sulfate and sulfanilamide (to final concentration, 10 ppm). Substances within the perivitelline space (including excess sperm) are liberated at rupture of the albumen membrane, frequently promoting fouling. Temperature block studies in which trochophore or veliger larvae were freed of contaminants by repeated transfer and then admitted to the tubes showed reduced mortality.

Haliotis rufescens larvae settled approximately 4 days after fertilization (18°C). However, after 3 wk in the temperature block, only those groups between 14° and 18°C had reached advanced postlarval stages (Figure 4). Settling occurred in some *H. corrugata* larvae within 3.5 days, but postlarvae did not survive (22°-23°C). Most rapid growth and best survival in *H. corrugata* was at 21°-22°C; the circular-shell postlarval stage was reached in 17 days (Figure 5). Settlement began in larvae of *H. fulgens* at 25.5°C in slightly less than 3 days, but again, subsequent success was poor. Those at 22°-23°C, however, settled by the fourth day and progressed to the circular-shell stage in 15 days (Figure 6). There was a close correspondence of curves for development rate vs. temperature obtained with progeny from different spawnings and parentage. Optima described graphically for each species varied within only 1°C for *H. corrugata*, 1.5°C for *H. fulgens*, and 2°C for *H. rufescens*.

Larvae introduced to a thermal gradient as operculate veligers exhibited tolerance to a broader temperature range. Subsequent development rate was, however, slowed. The general retardation may be a shock response to environmental change. The greatly reduced volume provided in the 20-ml tubes and the totally darkened conditions in the temperature block contrast with

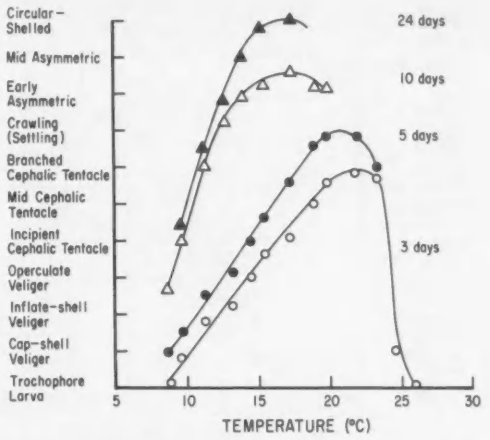

FIGURE 4.—Development of larvae of *Haliotis rufescens* at a series of temperatures when introduced to the thermal gradient as trochophores.

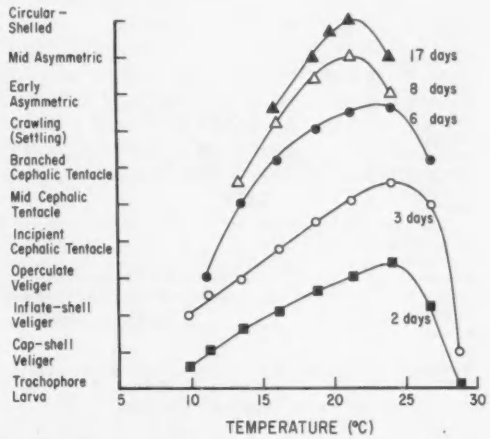

FIGURE 5.—Stages attained by larvae of *Haliotis corrugata* over a period of 17 days. Larvae were placed in the thermal gradient at the trochophore stage.

the 10-liter volume and illumination in the plastic rearing containers. In an experiment illustrating the point, *H. corrugata* eggs, trochophores and operculate veligers were placed in the gradient for 5 days in each case. At 20°-22°C, eggs developed rapidly and early postlarval stages reached in 5 days. However, operculate veligers had not yet reached the crawling stage at an age of 7 days (Figure 7).

In temperature block experiments, survival through settling usually ranged between 50 and

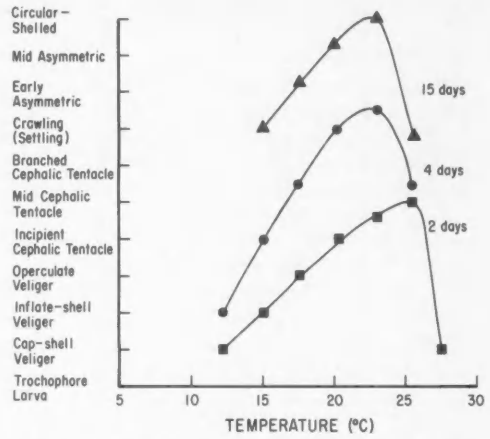

FIGURE 6.—Stages attained by *Haliotis fulgens* larvae incubated at several temperatures for 15 days. The experiment was initiated with trochophore larvae.

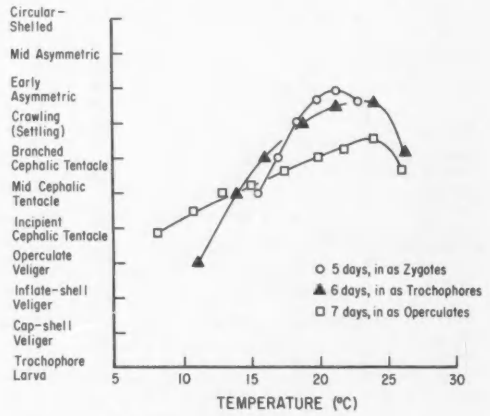

FIGURE 7.—Comparison of development rate and tolerated thermal range in larvae of *Haliotis corrugata* placed in the temperature block at 1, 20, and 48 h after fertilization.

80% within the physiologically acceptable temperature range. High mortality near the upper limit might have been due, in part, to oxygen exhaustion. This was tested by sampling open-top tubes in the block at 22° and 24°C for oxygen content after holding approximately 150 larvae (*H. rufescens*) for 48 h. A decline from 5.8 to 2.9 ml O_2/liter was observed at 22°C in 48 h. Routinely, therefore, only 25 to 50 larvae or eggs were admitted to each tube and once daily tubes were mixed to assure adequate oxygen was available. Subsequently oxygen depletion was not a cause of mortality.

THERMAL TOLERANCE OF POSTLARVAE

Postlarvae ranging in age from 1 to 2 mo were placed (2-5/tube) in the thermal gradient block and provided each 3-4 days a mixture of three species of diatoms (*Nitzschia* spp.). Tubes were checked for survival and growth of postlarvae over periods of 2 wk. Survival was good in all species at colder temperatures, but those at 10°-12°C invariably were lethargic and could not right themselves once overturned. *Haliotis rufescens* survived over the range 10°-19.5°C. *Haliotis corrugata* and *H. fulgens* were tolerant to the same lower temperatures but had different upper limits, 23.5° and 26.0°C, respectively. Typically survival was nearly 100% over a broad intermediate range of temperatures, but declined sharply within 2° of the extremes.

POSTLARVAL AND JUVENILE GROWTH

Specific differences in growth rate of both postlarvae and juveniles under laboratory conditions were measured. When its postlarvae were provided near optimal thermal and feeding environments, *H. fulgens* formed the first respiratory pore in about half the time required by the other species. As the pore is formed, a notch is first seen on the anterior right shell margin. The feature is conspicuous and serves as a convenient point of comparison. The "notch stage" was reached in some rapid-growing *H. fulgens* at an age of 30 days (Table 1).

Variability in growth rate was marked. Groups of juveniles of identical parentage, age, and rearing environment sampled periodically for shell length distribution reflected a broad range and age-increasing standard deviation (Table 2). Shell

TABLE 1.—Age and shell length of postlarval *Haliotis* at formation of the first respiratory pore.

Species	Age (days)	Shell length (mm)	Temperature (°C)
H. rufescens	60-70	1.5-1.8	14-18
H. corrugata	50-60	2.0-2.5	15-22
H. fulgens	30-40	1.7-2.0	16-24
H. sorenseni	55-65	2.0-2.1	[1]14-18

[1]Leighton, 1972.

length at 1 yr of age in four species reared in the laboratory varied over a range greater than 10mm (Table 3).

INFLUENCE OF TEMPERATURE ON GROWTH RATE OF JUVENILES

Several growth experiments were conducted with juveniles of the three species of abalones to gain comparative data and to establish respective temperatures of maximum growth rate. Juveniles were reared for month-long periods in 10-liter plastic containers held at six temperatures between 12° and 30°C. Both *H. corrugata* and *H. fulgens* displayed enhanced growth rate above 20°C. *Haliotis rufescens,* however, grew best below 20°C and, in fact, grew but slightly less at the coldest temperature, 12.5°C (Table 4, Figure 8). *H. fulgens* again showed a superior growth rate. While a mean daily shell growth approaching 90 μ was observed at its temperature of maximum growth rate (26°C), some individuals increased in shell length as much as 130 μ per day.

DISCUSSION

Seven species of *Haliotis* occur in southern California waters ranging vertically from the intertidal to depths over 35 m. Depth distribution is stratified specifically, although in certain areas (i.e., in the presence of localized upwelling) overlapping does occur. Vertical and latitudinal distribution appears most closely related to temperature. The Point Loma (San Diego) shelf from 0 to 35 m supports all California abalone species (Table 5). Colder water species may be found intertidally in northern California (*H. rufescens, H.*

TABLE 2.—Variation in size of juvenile *Haliotis* of identical parentage, age, and growing environment.

Species	Age (months)	Number	Shell length (mm) Mean	Range	SD
H. rufescens	3.7	18	4.4	2.6-6.1	1.06
H. corrugata	5.0	27	9.2	6.8-14.1	2.42
H. fulgens	4.7	70	7.1	3.6-12.0	2.00
H. sorenseni	3.3	19	4.3	3.0-5.6	0.64

TABLE 3.—Size of *Haliotis* at completion of first year growth in the laboratory.

Species	Shell length (mm) Mean	Range	Number
H. rufescens	15.6	9.9-20.0	50
H. corrugata	18.3	12.2-26.4	18
H. fulgens	32.8	30.5-38.9	[1]3
H. sorenseni	13.4	8.0-21.0	19

[1]Recent observations on growth of over 100 juvenile *H. fulgens* suggest the three individuals represented here were exceptionally rapid growers. Projection of growth of juveniles presently 8 mo old suggest the mean size at 1 yr under laboratory conditions may fall closer to 25 mm.

TABLE 4.—Daily shell elongation rate for groups of juvenile *Haliotis* reared for month-long periods at different temperatures (microns/day).

Species and date	Temperature (°C ± 1.5°) 12	15	18	21	24	27	30
H. rufescens							
Oct. 1971	91	61	90	45	32	([1])	
Jan. 1972	36	41	68	61	29		
Mar. 1972	70	64	84	79	35		
Dec. 1972	46	92	67	95	13		
Mean	60.9	64.5	77.3	70.0	27.3		
H. corrugata							
Jun. 1972	26	29	30	46	53		
May 1973	57	55	62	54	60	28	
Jun. 1973		45	72	91	63	68	14
Mean	41.5	43.0	54.7	63.7	58.7	48.0	14.0
H. fulgens							
Mar. 1973	23	29	63	77	119	64	
May 1973	21	21	55	74	88	114	
Jun. 1973		21	56	60	50	86	54
Mean	22.0	23.7	58.0	70.3	85.8	88.0	54.0

[1]*H. rufescens* did not survive in the 27°C containers.

These data are averages for groups of 8 to 15 individuals reared in each of six 10-liter plastic drums. In the case of *H. corrugata* and *H. fulgens,* temperatures were raised throughout for the third experiment to cover the supraoptimal range. Juveniles used in these experiments ranged from 5 to 20 mm.

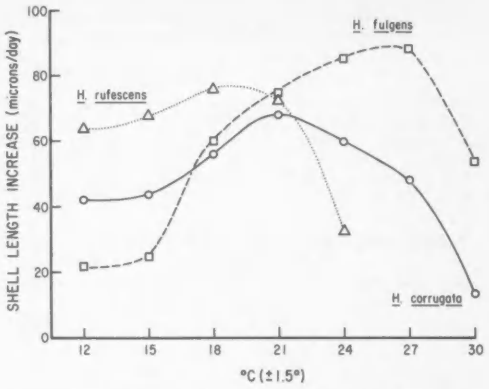

FIGURE 8.—Growth rate of juvenile abalone held for month-long periods at different temperatures. Points are averages for groups of 8 to 15 individuals (see Table 4).

TABLE 5.—Approximate depth distribution of *Haliotis* species off Point Loma (San Diego, Calif.).

Species	Depth range (m)
H. cracherodii	0-2
H. fulgens	0-5
H. corrugata	1-20
H. rufescens	10-25
H. k. assimilis	10-30
H. sorenseni	15-35
H. walallensis	15-35

kamtschatkana, and *H. walallensis* together with the generally shallow water and intertidal *H. cracherodii*). *Haliotis sorenseni*, *H. corrugata*, and *H. fulgens* range from Pt. Conception to central Baja California. *Haliotis cracherodii* and *H. rufescens* occur throughout California and northern Baja California, while *H. k. assimilis* replaces *H. kamtschatkana* in southern California (McLean, 1966).

This study has shown that the thermal requirements, particularly for eggs and early larvae, are exacting. Field distribution of juvenile and adult members of each species correspond with the thermal tolerance range observed in larvae in the laboratory. The range of tolerance increased with larval age. Larvae of *H. corrugata* placed in the thermal gradient as operculate veligers survived a range of 18° (from 8° to 26°C), while those resulting from eggs placed in the same situation were tolerant of a range of only 8° (from 15° to 23°C). The observation is not new nor limited to *Haliotis* (Loosanoff and Davis, 1963). Thus, survival of larvae dispersed in nature is likely dependent on their remaining within a water mass of appropriate temperature and further, settling in areas over which temperature change will not be extreme. Recruitment to marginal environments may rely on the timely influx of advanced veliger larvae. The situation is complicated, no doubt, by acclimation of mature adults near distribution limits.

Most studies in abalone culture have been conducted by Japanese workers concentrating on the species native to northern Japan, *H. discus hannai*. Its broad thermal tolerance (approximately 5°-30°C) and relatively rapid growth at elevated temperatures have attracted the interest of mariculturists. The species exhibits rapid larval development, settling in 3 days at 25°C and reaching the notch stage in 42 days (Kan-no and Kikuchi, 1962). When reared at five temperatures between 5° and 25°C, juvenile *H. d. hannai* displayed daily increments in shell length of 1, 2, 32, 68, and 95 μ, respectively, according to the same report. During winter months when sea temperatures at the coastal hatchery drop below 10°C, cultured juvenile abalone are transferred to a site adjacent the Yogasaki Electric Generating Plant using 26°C water detoured from the effluent stream (Kan-no, pers. commun., McBeth, 1972).

Thermal tolerance and growth characteristics of larvae and juveniles of the Japanese species are similar to that observed in the present study in *H. fulgens*. Of the American species considered here, only *H. fulgens* could be recommended for heated effluent mariculture.

First year growth measured in this study is not considered to approximate growth in nature. Artificial lighting, synthetic materials in rearing tanks, and other factors may have influenced growth, and the growth rate estimates are likely conservative. The general observation of rapid, moderate, and slow growth in *H. fulgens*, *H. rufescens* and *H. corrugata*, respectively, is concluded to reflect specific differences in growth potential.

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LABORATORY STUDY OF BEHAVIORAL INTERACTIONS BETWEEN THE AMERICAN LOBSTER, *HOMARUS AMERICANUS*, AND THE CALIFORNIA SPINY LOBSTER, *PANULIRUS INTERRUPTUS*, WITH COMPARATIVE OBSERVATIONS ON THE ROCK CRAB, *CANCER ANTENNARIUS*[1]

C. O'Neil Krekorian, David C. Sommerville, and Richard F. Ford[2]

ABSTRACT

Behavioral interactions between *Homarus americanus* and *Panulirus interruptus*, with comparative observations on *Cancer antennarius*, were studied in order to determine the possible effects an introduced population of *H. americanus* would have on the southern California population of *P. interruptus*. Subjects were placed in tanks 3 m in diameter with observational windows equally spaced around the tank perimeter. Three 30-min observation periods were conducted on the lobsters each day for a 5-day precontrol period (*H. americanus* absent), a 10-day experimental period (*H. americanus* present), and a 5-day postcontrol period (*H. americanus* absent). Five replicates of a shelter and no shelter condition were made with five naive *P. interruptus* and one *H. americanus* for each replicate. Agonistic action patterns were recorded for actors and reactors, along with various other behaviors, on data sheets partitioned into 1-min intervals. A large percentage of *Homarus*-initiated behavioral actions in the shelter (44%) and no shelter (39%) conditions involved threat and attack by *H. americanus*. In *Homarus*-initiated interactions, *P. interruptus* was displaced by *H. americanus* 61% of the time in the shelter condition and 63% of the time in the no shelter condition. Although *Panulirus*-initiated interactions occurred much less frequently, the results were similar to the *Homarus*-initiated interactions in that *P. interruptus* was ultimately displaced by threatening and attacking *H. americanus* 92% of the time in the shelter condition and 76% of the time in the no shelter condition. Our results, and those of other studies, are discussed with respect to the potential adverse effects of introducing *H. americanus* into southern California waters. The evidence suggests that such an introduction is inadvisable.

At the present time, there is strong interest from the private sector in introducing the American lobster, *Homarus americanus*, into California waters. This interest arises primarily from the marked downward trend in annual landings of the California spiny lobster, *Panulirus interruptus*, and the high unit value and continuing demand for lobster species in general and in particular for the American lobster, which supports one of the most valuable fisheries in North America. Conditions along the entire California coast appear well within the limits tolerated by larvae, juveniles, and adults of *H. americanus*. Thus, with the recent development of successful mass culture techniques (Hughes, 1968; Ghelardi and Shoop, 1968; Kensler, 1970), the species probably could be established, at least by means of continued stocking (Ghelardi and Shoop, 1972).

Despite the apparent value of the American lobster as a Pacific Coast fishery, there are several potential detrimental effects of introducing it into the Pacific which must be considered (Rathbun, 1888; Ghelardi, 1967). These are: 1) the introduction of disease, parasitic organisms, or other microfauna and microflora harmful to native species and 2) the elimination or reduction in abundance of ecologically similar forms, such as *P. interruptus*, in areas where *H. americanus* might become established.

Introductions of some foreign animals and plants have had very serious effects on native species (Elton, 1958). Thus, there is a great need for effective evaluation and control of exotic species introductions, as recently discussed by Lachner, Robins, and Courtenay (1970). There have been at least 23 attempts to introduce

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[2]Biological Sciences, San Diego State University, San Diego, CA 92115.

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H. americanus between Monterey Bay and British Columbia (Ghelardi and Shoop, 1968). The exact reasons for the failure of these introductions are unknown. However, three possible causes were: 1) low stocking density, 2) unsuitability of the locations used for introductions, and 3) possible injuring or weakening of lobsters through mishandling or disease before the introductions (Ghelardi and Shoop, 1968). In the lobster transplants, as in virtually all other attempts to transplant species, there has been little or no effort to evaluate the impact the exotic would have on native species or to control pathogens and other potentially harmful organisms associated with it. Only the recent pilot introduction in British Columbia by Ghelardi and Shoop (Ghelardi, 1967; Ghelardi and Shoop, 1972) considered potential detrimental effects and was conducted on a truly scientific basis.

While it might be argued that one can never determine what the effects of an exotic introduction will be until it takes place, we feel that a serious attempt must be made to evaluate potential adverse effects by laboratory studies before even a small-scale pilot transplant is attempted. During the period 1970-73 we, and others of our group, have conducted a series of studies on the social interactions of *H. americanus* with ecologically similar decapod crustaceans from southern California waters. This paper describes the results of one of our studies concerning interactions between *H. americanus* and *P. interruptus* with comparative observations on *P. interruptus* and the rock crab, *Cancer antennarius*. In it, we have primarily considered agonistic interactions. Other studies have shown that interspecific aggression can be important in regulating the lives of sympatric species (see Aspey, 1971; also Myreberg, 1972a).

METHODS AND MATERIALS

American lobsters were purchased in San Diego from the Gulf of Maine Lobster Corporation. They were quarantined 2 wk in a large holding tank (0.5 × 1.2 × 2.3 m) for effects of gaffkemia or other diseases before being introduced to experimental tanks. California spiny lobsters and rock crabs were trapped in shallow water off the San Diego coast and were either introduced directly into experimental tanks or maintained for short periods in holding tanks of the same size employed for *H. americanus*.

Holding tanks were supplied with fresh running seawater from the Scripps Institution system. The temperature of the water in tanks varied throughout the year in close correspondence with ambient ocean temperatures, from a minimum of 14°C in January to a maximum of 23°C in August. The study began in July 1972 and ended in April 1973. Lobsters and crabs in holding tanks were fed frozen squid, *Loligo opalescens*, and northern anchovy, *Engraulis mordax*, twice a week. No attempt was made to control the photoperiod for these individuals while in the holding tanks. However, they were exposed to the normal day-night cycle during this period from light entering through the walls, roof, and building openings.

Three experimental tanks were used, each 3.04 m in diameter and 1.22 m in height, with a capacity of approximately 9,000 liters. Each tank had four observation windows 68.5 × 48.0 cm positioned equidistant around the perimeter. The tanks were enclosed in lightproof tents made of black Mobil Kordite[3] polyethylene sheeting of 6-mil thickness. Lobsters in the experimental tanks received 11 h of light daily from 0400 to 1500 P.s.t. (Pacific standard time), supplied by two 75-W General Electric floodlights. The experimental subjects were not fed while in the experimental tanks so as to eliminate the variable of interactions for food.

Three experimental conditions were studied. These were: 1) social interaction between *P. interruptus* and *H. americanus* in the absence of shelter, 2) social interaction between *P. interruptus* and *H. americanus* with more shelters than lobsters, and 3) social interaction between *P. interruptus* and *C. antennarius* without shelter. Seven shelters were provided for the experimental condition involving interaction between *P. interruptus* and *H. americanus* with shelter. The shelters, which measured 25 cm in width, 38 cm in length, and 14 cm in height, were made by cutting 76-cm sections of concrete conduit lengthwise and then into 38-cm lengths.

In each experimental condition, five California spiny lobsters and either one American lobster or one rock crab were employed. Five replicates of each experimental condition were made using naive animals for each replicate. The 5:1 ratio used for the *P. interruptus* and *H. americanus*

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

interactions was a compromise between a representative density which might result from a large stocking of *H. americanus* in natural habitats on the southern California coast and the physical limitations of the experimental tanks which prevented using more *P. interruptus*. Both males and females of each lobster species were used for experiments. However, only male *C. antennarius* were used because all females obtained were carrying eggs at the time these experiments were conducted.

Interaction experiments involving *P. interruptus* and *C. antennarius* were employed to help in the process of assessing potential effects *H. americanus* might have on *P. interruptus*. That is, we wanted to establish a behavioral base line by using a clawed decapod crustacean which is naturally sympatric with *P. interruptus*. Thus, the 5:1 ratio used for the *C. antennarius* and *P. interruptus* interactions was employed for comparative purposes.

The *P. interruptus* subjects used ranged in weight from 209 to 911 g, with a mean of 436 g. *Homarus americanus* used weighed from 417 to 635 g, with a mean of 471 g. *Cancer antennarius* used ranged in weight from 560 to 840 g, with a mean of 673 g. California spiny lobsters were assigned to groups by a randomization process. Each group usually consisted of both sexes and individuals which were larger, smaller, and the same size as the single American lobster tested. *Cancer antennarius* used in the experiments weighed more than most of the California spiny lobster subjects with which it was tested. An attempt was made to use *P. interruptus* that weighed between 400 and 600 g for all experiments so that their weight matched the weight of the *H. americanus* available to us. As a result of poor trap catches, however, we were sometimes forced to use *P. interruptus* that were either smaller or larger than the *H. americanus* subjects.

Each of the 15 separate experiments consisted of three observation periods. These were called the precontrol, experimental, and postcontrol periods. For the social interaction experiments involving *P. interruptus* and *H. americanus*, precontrol observations were taken for 5 days, experimental observations were taken for 10 days, and postcontrol observations were taken for 5 days. For the experiments involving social interactions between *P. interruptus* and *C. antennarius*, the precontrol, experimental, and postcontrol observation periods were all 5 days in duration. For the precontrol observation period, only individuals of *P. interruptus* were present in the experimental tanks. Upon completion of the precontrol period, an *H. americanus* or *C. antennarius* was introduced into the tank. Following the experimental observation period, the *H. americanus* or *C. antennarius* was removed and the postcontrol observations of *P. interruptus* taken.

For *P. interruptus* and *H. americanus* experiments, three 30-min observation periods were conducted daily for each tank. These 30-min observation periods were taken between 0800 and 1000 (4-6 h after the onset of the lights), 1200 and 1400 (8-10 h after the onset of the lights), and 1510 and 1700 h (10 min-1 h 50 min after the lights went off) P.s.t. for precontrol, experimental, and postcontrol periods. In the experiment involving *P. interruptus* and *C. antennarius*, only two 20-min observation periods were taken daily. One was taken between 0800 and 1000 and the other between 1510 and 1700. The 1200-1400 observation period was omitted because of the low frequency of interactions shown by these species during initial observations. Table 1 summarizes the experimental paradigm used for this study.

Observations taken between 1510 and 1700 were made using two 100-W red lights with a spectral distribution between 550 and 720 nm. Most of the red light (75%) fell within 600-650 nm. Spectral sensitivity of *H. americanus* ranges from 400 to 600 nm with peak sensitivity at 520-525 nm (Kennedy and Bruno, 1961). At present no information exists on the spectral sensitivity of *P. interruptus*, but the assumption was made that this species also is insensitive to light within this spectral range. During the study, we observed no evidence that movement and social behavior of either species was inhibited by the use of red lights.

TERMINOLOGY

The frequency and type of behavioral interactions between *P. interruptus* and *H. americanus* or *C. antennarius* were recorded on a data sheet which was partitioned into 1-min intervals. The behavior of the actor (the individual presenting the stimuli or initiating the interaction) and the subsequent response of the reactor (the individual

TABLE 1.—Experimental paradigm for social interaction study between *Homarus americanus*, *Panulirus interruptus*, and *Cancer antennarius*

Experimental condition	Precontrol			Experimental			Postcontrol		
	Number of days	Length of observation periods (min)	Time of observations	Number of days	Length of observation periods (min)	Time of observations	Number of days	Length of observation periods (min)	Time of observations
H. americanus vs. *P. interruptus* No shelter	5	30	0800-1000 1200-1400 1510-1700	10	30	0800-1000 1200-1400 1510-1700	5	30	0800-1000 1200-1400 1510-1700
H. americanus vs. *P. interruptus* Shelter	5	30	0800-1000 1200-1400 1510-1700	10	30	0800-1000 1200-1400 1510-1700	5	30	0800-1000 1200-1400 1510-1700
P. interruptus vs. *C. antennarius* No shelter	5	20	0800-1000 1510-1700	5	20	0800-1000 1510-1700	5	20	0800-1000 1510-1700

responding to the stimuli) were both recorded in the predetermined categories described below. In addition, the amount of locomotion displayed by subjects, their location in the tank with respect to the wall, and the number of individuals in shelters, when present, were recorded. The behavioral action patterns of *P. interruptus*, *H. americanus*, and *C. antennarius* described by previous workers were employed in this study where possible.

I. The following categories were employed for the actor: A) Approach, B) Threat, C) Attack, and D) Social contact. These terms are defined, in most cases, separately for each of the three species considered.

A) Approach—Movement of the actor directly toward a moving or stationary heterospecific. During approach, the actor compensates for changes in the direction of movement of a moving heterospecific so that the actor is always moving directly toward the heterospecific. No implication of function is intended in our use of the term approach.

B) Threat

1) *Homarus americanus*

Meral spread—In this study only the display described by Schrivener (1971) as meral spread was recorded as threat. Schrivener's description of this behavior is as follows: "During meral spread, the lobster stands on its walking legs with its body raised from 4 to 5 cm off the bottom. The abdomen is usually fully extended, with the cephalothorax angled slightly upwards from the horizontal. The chelae are held about 5 cm off the bottom spread wide apart with their long axes pointing directly at the opponent. Some animals hold the claws fully extended, wide apart, and as high off the bottom as possible."

2) *Cancer antennarius*

Lateral Merus Display—The merus of the chelipeds is extended laterally, with the distal end of the meri raised and extended somewhat anteriorad. The higher the intensity of the display, the greater is the lateral spreading of the chelipeds (Schone, 1968; Wright, 1968). Wright (1968) subdivides the Lateral Merus Display into three subtypes based on the position of the chelae. These are: 1) the High-Intensity Merus Display in which the chelae are unflexed (maximum adduction) with the tips held laterally; 2) the Mid-Intensity Merus Display in which the chelae are half flexed so that the tips point forward; and 3) the Low-Intensity Merus Display in which the chelae are flexed, with their tips medial. All intensities of the meral spread were observed, but these were simply recorded together as threat in our study.

3) *Panulirus interruptus*
Two of the aggressive postures described by Roth (1972) were used in this study. These aggressive postures are body raise and rear-up. We observed that these are the most common and morphologically distinct aggressive postures exhibited by *P. interruptus*.
   a) Body raise—Raising the body off the substrate by partial extension of the walking legs. This corresponds to Roth's term Rise Up (R_1).
   b) Rear-up—Raising the body off the substrate by full extension of the third, fourth, and fifth walking legs. The anterior part of the body is raised much higher than the posterior part of the body. This was also called Rise Up by Roth (R_2 and R_3). However, we have combined his R_2 and R_3 into a separate category, rear-up, because they appear to be different intensities of the same behavior action pattern, which is distinct from R_1.

C) Attack
   1) *Homarus americanus* and *Cancer antennarius*
   Four actions were included under attack. These were pinch, push, scissoring, and chase.
      a) Pinch—Rapid gripping and release of any part of a California spiny lobster's body with one or both chelipeds.
      b) Push—Contact between the chelipeds and any part of a California spiny lobster's body when the chelipeds are thrust forward while the body remains stationary or the chelipeds are extended or in a meral spread in a stationary position during locomotion.
      c) Scissoring—As described by Schrivener (1971) for *H. americanus*, "This occurs when one lobster faces its opponent, with the chelae in the meral spread posture (spread wide apart, long axes of the palms pointing at the adversary). The chelae are then rapidly brought together in a scissoring motion. As a result, they either strike or pass rapidly in front of the other animal."
      d) Chase—During chase the actor moves rapidly toward a heterospecific that in turn is usually moving rapidly and is obviously trying to remove itself from the vicinity of the lobster following it. Chase was recorded only after the actor and reactor had been within 30 cm from one another. Frequently, chase precedes a push or pinch and follows an initial lunge by an actor towards the reactor. During chase *H. americanus* usually displays meral spread.
   2) *Panulirus interruptus*
   Two actions were included under attack. These were physical contact and chase.
      a) Physical contact—This involves colliding with some part of a heterospecific's body; in some cases clasping of the opponent with the first three pairs of walking legs or a bite may occur. This includes Roth's (1972) low intensity attack (A_1), high intensity attack (A_2), and clasp (CL).
      b) Chase—Rapid locomotion toward a reactor while it is removing itself from the vicinity of the lobster following it.

D) Social contact—Two heterospecifics were recorded as having social contact when one of the following events occurred.
   1) Two or more heterospecifics came within 30 cm of one another during movement about the tank without aggressive interaction occurring. This category was recorded

whether one or both animals were moving, and in some cases direct physical contact was made.

2) Two or more heterospecifics were touching or within 30 cm of one another, were not moving, and exhibited no aggressive interaction. Social contact during movement was distinguished from approach by the absence of direct movement of heterospecifics toward one another. That is, the animals were not on a collision course.

II. The following categories were employed for the reactor: A) No response, B) Walk away, C) Abdomen flex, D) Threat, and E) Attack.

A) No response—No change in the overt behavior of the reactor.

B) Walk away—Movement away from an approaching, threatening, or attacking heterospecific, using the walking legs.

C) Abdomen flex—Movement away from an approaching, threatening, or attacking heterospecific, using rapid flexion of the abdomen.

D) Threat—The description(s) of threat used for *H. americanus*, *P. interruptus*, and *C. antennarius* provided above for actors (I-B) was also used for the reactor.

E) Attack—The description(s) of attack used for *H. americanus*, *P. interruptus*, and *C. antennarius* provided above for actors (I-C) was also used here for the reactor.

III. Additional categories used on the data sheet and their definitions were as follows:

A) Roaming—Slow or moderate walking about the tank. During roaming, direct interaction between heterospecifics or conspecifics does not occur. For *P. interruptus*, roaming by an individual was recorded only if it occurred for 31 s or more during a 1-min interval. For *H. americanus* and *C. antennarius*, the amount of time they were observed roaming during each 1-min interval was recorded.

B) Wall—Like many decapods, *P. interruptus* exhibits thigmotactic behavior. When shelter is absent individuals are found with their bodies in contact with a solid object. In our no shelter condition, the tank wall was the only solid object present. A lobster that had some part of its body, excluding the antennae, within 30 cm of the side of the tank for 31 s or more of each 1-min interval was recorded as wall. The location of a lobster within the tank that was greater than 30 cm from the side of the tank for 31 s or more of each 1-min interval was recorded as no wall.

C) Group—A congregation of two or more subjects, each within 30 cm of one another. Thus, in a group of five *P. interruptus*, a maximum distance of 120 cm would separate lobsters at opposite ends of a group.

RESULTS AND DISCUSSION

Agonistic Behavior

The frequency and outcome of agonistic behavioral interactions between *H. americanus* and *P. interruptus* for conditions involving shelter and no shelter are shown in Table 2. Similar data also are presented in this table for interactions between *P. interruptus* and *C. antennarius*.

Homarus vs. *Panulirus* with No Shelter

There were a total of 2,515 *Homarus*-initiated behavioral interactions by actors for the five replicate *H. americanus-P. interruptus* no shelter experiments. Twenty percent of the behavioral interactions were classed as social contact, 40% as *Homarus* approach, 24% as *Homarus* threat, and 15% as *Homarus* attack (Table 2). Sixty-eight percent (1,700) of the *Homarus*-initiated behavioral interactions occurred during the 1510-1700 h observation period (lights off).

There were a total of 1,683 responses by reactors to *Homarus*-initiated interactions. Thirty seven percent of these were classed as no response, 49% *Panulirus* walk away, and 14% *Panulirus* abdomen flex (Table 2). Thus, *P. interruptus* was displaced a total of 63% of the time when *H. americanus* initiated a behavioral interaction. *Panulirus interruptus* was never observed to threaten or attack *H. americanus* in *Homarus*-initiated behavioral interactions.

A total of 227 *Panulirus*-initiated behavioral interactions were recorded in the five replicate

TABLE 2.—The total number of behavioral interactions between *Homarus americanus* and *Panulirus interruptus* during 10-day experimental periods for the shelter (n = 5 groups) and no shelter (n = 5 groups) conditions, and between *P. interruptus* and *Cancer antennarius* during 5-day periods for a no shelter condition (n = 5 groups). Social contact (SC) and no response (NR) for *Homarus*-initiated interactions include both *Homarus* and *Panulirus* actions where only social contact occurred. HA = *Homarus* approach; HT = *Homarus* threat; HAT = *Homarus* attack; PWA = *Panulirus* walk away; PAF = *Panulirus* abdomen flex; PA = *Panulirus* approach; PT = *Panulirus* threat; PAT = *Panulirus* attack; HWA = *Homarus* walk away; HAF = *Homarus* abdomen flex; CA = *Cancer* approach; CT = *Cancer* threat; CAT = *Cancer* attack; CWA = *Cancer* walk away.

Homarus-initiated interactions

		Actor					Reactor			
P.s.t.	Experimental condition	SC	HA	HT	HAT		NR	PWA	PAF	
0800	No shelter	177	172	106	56		207	156	24	
	Shelter	7	6	1	2		8	5	1	
1200	No shelter	97	97	63	47		128	92	43	
	Shelter	6	2	1	1		7	3	1	
1510	No shelter	238	748	438	276	Σ = 1,700 (68%)	299	572	162	Σ = 1,033 (61%)
	Shelter	24	104	74	41	Σ = 243 (90%)	53	72	27	Σ = 152 (86%)
Totals	No shelter	512	1,017	607	379	Σ = 2,515	634	820	229	Σ = 1,683
	Percent	20	40	24	15		37	49	14	
	Shelter	37	112	76	44	Σ = 269	68	80	29	Σ = 177
	Percent	14	42	28	16		38	45	16	

Panulirus-initiated interactions

		Actor			Reactor				
P.s.t.	Experimental condition	PA	PT	PAT	NR	HWA	HAF	HT	HAT
0800	No shelter	36	0	0	3	1	0	29	16
	Shelter	3	0	0	0	0	0	3	0
1200	No shelter	83.	1	0	7	3	1	65	26
	Shelter	3	0	0	1	0	0	2	1
1510	No shelter	107	0	0	6	41	4	54	21
	Shelter	22	0	0	0	2	0	20	5
Totals	No shelter	226	1	0	16	45	5	148	63
	Percent	100	0	0	6	16	2	53	23
	Shelter	28	0	0	1	2	0	25	6
	Percent	100	0	0	3	6	0	74	18

Cancer-Panulirus interactions

		Actor							Reactor							
P.s.t.	Experimental condition	SC	CA	PA	CT	PT	CAT		NR	CWA	PWA	PAF	CT	PT	CAT	
0800		130	4	16	2	0	5		145	0	6	0	2	0	2	
1510		37	8	20	2	3	2		49	0	15	0	9	0	3	
Total	No shelter	167	12	36	4	3	7	Σ = 229	194	0	21	0	11	0	5	Σ = 231
	Percent	73	5	16	2	1	3		84	0	9	0	5	0	2	

experiments. Of these, 226 were *Panulirus* approach while only 1 was *Panulirus* threat (Table 2). There was a total of 277 responses by the reactors (*Homarus*). Sixteen (6%) of these were classed as no response, 45 (16%) as *Homarus* walk away, 5 (2%) as *Homarus* abdomen flex, 148 (53%) as *Homarus* threat, and 63 (23%) as *Homarus* attack (Table 2). Thus, 76% of *H. americanus* responses to *P. interruptus* approach were threat and attack. These threats and attacks by *H. americanus* subsequently resulted in displacement of *P. interruptus* from the immediate area.

The number of behavioral actions by both the actor (primarily *Homarus*) and reactor (primarily *Panulirus*) decreased with time, as shown in Table

3. There was a significant reduction in *Homarus*-initiated actions with time as indicated by the results of a Spearman Rank Correlation Analysis ($r_s = -0.66$, $P < 0.05$; Siegel, 1956). Social contact was excluded from the statistical analysis of actor actions because it included and did not differentiate *H. americanus* and *P. interruptus*-initiated interactions. Most social contact, however, was initiated by *H. americanus*. There also was a significant decrease in behavioral actions with time for *P. interruptus* responses ($r_s = -0.82$, $P < 0.01$). Only *Panulirus* walk away and abdomen flex were considered. No response was excluded from the statistical analysis of reactor actions because it included both *H. americanus* and *P. interruptus* responses.

In the absence of shelter, some *H. americanus* excavated a depression in the sand where they remained when they were not roaming. When a *P. interruptus* approached an *H. americanus* in its sand depression, the likelihood of attack increased, and the attacks appeared to last longer and involve more pinching.

Homarus vs. *Panulirus* with Shelter

The addition of seven shelters reduced the number of *Homarus*-initiated interactions as compared with the no shelter condition. A comparison of all *Homarus*-initiated interactions (both actor and reactor) between the shelter and no shelter conditions indicated that *Homarus*-initiated interactions for the shelter condition were significantly reduced ($P = 0.01$, Wilcoxon matched-pairs test; Siegel, 1956). There were a total of 269 behavioral actions by actors and 177 by reactors (Table 2). Ninety percent (243) of the behavioral actions by actors and 86% (152) of behavioral actions by the reactors occurred in the 1510-1700 h observation period.

Fourteen percent of the *Homarus*-initiated interactions of actors were classed as social contact, 42% as *Homarus* approach, 28% as *Homarus* threat, and 16% as *Homarus* attack. The behavioral actions of the reactors were 38% no response, 45% *Panulirus* walk away, and 16% *Panulirus* abdomen flex.

There was a total of 28 *Panulirus*-initiated behavioral actions for the five replicate experiments. All were classed as *Panulirus* approach. Thirty-four behavioral actions by *H. americanus* (reactor) resulted. Of these, 1 was classed no response, 2 *Homarus* walk away, 25 *Homarus* threat, and 6 *Homarus* attack. Thus, 92% of these responses of *H. americanus* to *Panulirus* approach involved threat and attack.

Most of the behavioral interactions that occurred in the *Homarus-Panulirus* shelter condition took place when the lobsters were out of their shelters. On some occasions, however, *H. americanus* attacked *P. interruptus* while they were in shelters. When this occurred *H. americanus* entered the shelter through the front entrance, the attack ensued, and *P. interruptus* fled through the back entrance which was nearly flush against the side of the tank. The amount of time *H. americanus* remained in the shelter of the displaced *P. interruptus* varied greatly. Some *H. americanus* left the shelter within 1 min and either roamed or displaced another *P. interruptus* from its shelter. Others remained in the shelter longer, and some for the duration of the observation period. *Panulirus interruptus* that approached *H. americanus* in a shelter were usually

TABLE 3.—The total number of *Homarus americanus*-initiated behavioral interactions with *Panulirus interruptus* by day for the no shelter condition ($n = 5$ groups). These totals include data from morning, noon, and evening observations. Social contact (SC) and no response (NR) totals include both *H. americanus* and *P. interruptus* actions. However, the great majority of SC is *Homarus* initiated, and the great majority of NR is derived from *Panulirus*. HA = *Homarus* approach; HT = *Homarus* threat; HAT = *Homarus* attack; PWA = *Panulirus* walk away; PAF = *Panulirus* abdomen flex.

	Actor						Reactor				
Day	SC	HA	HT	HAT	Total	Total[1]	NR	PWA	PAF	Total	Total[2]
1	113	234	116	65	528	415	146	185	38	369	223
2	48	112	93	61	314	266	59	92	22	173	114
3	25	85	56	37	203	178	32	78	29	139	107
4	32	85	73	55	245	213	42	72	28	142	100
5	49	79	18	15	161	112	53	68	12	133	80
6	40	92	51	26	209	169	45	84	16	145	100
7	37	108	59	36	240	203	54	72	29	155	101
8	93	109	72	48	322	229	105	75	32	212	107
9	53	75	46	19	193	140	66	65	10	141	75
10	22	38	23	17	100	78	34	29	13	76	42

[1]These totals exclude SC.
[2]These totals exclude NR.

quickly threatened or attacked. However, this event was rare.

When *H. americanus* pinched *P. interruptus*, in both the shelter and no shelter condition, the pincer claw appeared to be the only one used. *Panulirus interruptus* that had been attacked, and especially those pinched by *H. americanus*, appeared to move away from an approaching *Homarus* in subsequent encounters at greater distances than they did initially before they had been attacked.

Panulirus vs. *Cancer* with No Shelter

There was little aggression shown in behavioral interactions between *P. interruptus* and *C. antennarius*, species which commonly occur together in nature. A total of 229 behavioral actions were initiated by actors. Of these, 73% (167) were classed as social contact, 5% (12) as *Cancer* approach, 16% (36) as *Panulirus* approach, 2% (4) as *Cancer* threat, 1% (3) as *Panulirus* threat and 3% (7) as *Cancer* attack (Table 2). There was a total of 231 responses by the reactors. Eighty-four percent (194) of these were classed as no response, 9% (21) were classed as *Panulirus* walk away, 5% (11) as *Cancer* threat, and 2% (5) as *Cancer* attack.

One of us (Krekorian) observed *P. interruptus* walk over *C. antennarius* 21 times with no response from the latter species. This was never observed between *P. interruptus* and *H. americanus*. In addition, on 63 occasions noninteracting groups were observed composed of two or more *P. interruptus* and *C. antennarius* within 30 cm of one another, and on 50 other occasions similar groups were observed consisting of *C. antennarius* and one *P. interruptus*. In contrast, we never observed groups composed of *H. americanus* and *P. interruptus*.

Discussion of Agonistic Behavior

These results show that a large percentage of *Homarus*-initiated behavioral interactions in the shelter (44%) and no shelter (39%) conditions involved aggressive behavior (*Homarus* threat + *Homarus* attack, Table 2). The response of *P. interruptus* to *Homarus* approach and aggressive acts was usually defensive. In the shelter condition *P. interruptus* was displaced by *H. americanus* 61% of the time. *Panulirus* either walked away or used an abdomen flex to remove itself from the area occupied by *Homarus*. In the no shelter condition *P. interruptus* was displaced 63% of the time. Although shelter reduced the total number of behavioral interactions initiated by *H. americanus*, the percentages for aggressive and defensive acts remained about the same (Table 2).

The number of *Panulirus*-initiated behavioral interactions was far less than the number of behavioral interactions initiated by *Homarus*. However, the result of the interactions which followed were qualitatively the same. That is, *P. interruptus* was ultimately displaced by threatening and attacking *H. americanus* in the shelter (92% of the time) and no shelter (76% of the time) conditions.

Grasping of one *H. americanus* by another was rarely involved in the agonistic encounters observed by Schrivener (1971). In contrast to this, we frequently observed *H. americanus* pinching *P. interruptus*. Pinching by *H. americanus* is typical of its predation behavior. At no time in our study did we observe *P. interruptus* attack *H. americanus* or *C. antennarius*.

Studies by other members of our group have shown that the laboratory activity rhythms of *P. interruptus* and *H. americanus* over a 24-h period are very similar, both species exhibiting their highest levels of activity during the first 4 h of darkness (Van Olst and Carlberg, pers. commun.). This similarity in the timing of activity probably would intensify interactions between the two species in the field. Such interactions could result in *P. interruptus* being displaced from areas occupied or frequented by *H. americanus*, and/or being placed under considerable stress due to possible competition for food, suitable refuges, or other aspects of space within the habitat. In the laboratory, *H. americanus* displaced *P. interruptus* when there was only one shelter for two lobsters (Lester, pers. commun.) and inhibited *P. interruptus* from feeding when food was limited (Needham, pers. commun.).

Assuming that the behavior displayed by the two lobster species in the laboratory would be similar to that occurring in the field, one would expect considerable agonistic interaction between the two species if they were to occupy the same habitat. Although there have been few studies that have thoroughly compared the behavior of animals in the laboratory with their behavior in the field, there are some data that suggest the

two are very similar, at least where species other than primates are involved. For example, a recent study by Myrberg (1972b), involving such a direct comparison, showed that the agonistic and other social behavior of the bicolor damselfish, *Eupomacentrus partitus*, in the laboratory was very similar to its field behavior both qualitatively and quantitatively. In another study, Hazlett and Bossert (1965) similarly detected no qualitative differences between the laboratory and field behavior of some pagurid and diogenid crabs. As a result of this, they chose to study the behavior of these crabs in the laboratory where conditions were more uniform and controllable.

There have been surprisingly few studies concerned with interspecific aggression. This is especially true of many decapod crustaceans for which most of the studies have been rather superficial (Reese, 1964). It is rapidly becoming apparent from the few studies that have been made, however, that interspecific aggression may be very important in regulating the distribution and abundance of many marine animal populations. Myrberg (1972a) has found that in the bicolor damselfish interspecific chases accounted for approximately 40% or more of the chases carried out by territorial males. Interspecific aggression was displayed by both sexes and occurred throughout the year.

In laboratory experiments, Teal (1958) found that the fiddler crab, *Uca pugnax*, reduced the number of burrows dug by *U. pugilator* and *U. minax*. In field studies, described by Aspey (1971), it was found that where *U. pugnax* and *U. pugilator* existed in overlapping areas, the number of burrows per square meter was significantly less than in areas inhabited only by *U. pugilator*. The reduction in the number of burrows dug by other species of *Uca* when paired with *U. pugnax* appears to be due to the greater frequency of agonistic display exhibited by *U. pugnax* (Aspey, 1971).

In contrast to the results of the *Panulirus-Homarus* experiments, very little behavioral interaction or aggression occurred between *C. antennarius* and *P. interruptus*. Seventy-three percent of actor behavior involved nonaggressive actions (social contact), and 84% of the reactor responses involved no change in behavior (no response). In addition, *C. antennarius* frequently remained in close proximity to *P. interruptus*, and *P. interruptus* frequently walked over *C. antennarius* when moving from one area in the tank to another area. These events were never observed in *Homarus-Panulirus* experiments. The laboratory observations on *Panulirus-Cancer* interactions agree with observations made in the field where *C. antennarius* is sometimes found sharing the same refuges with *P. interruptus*.

Our data also show that even though the number of *Homarus-Panulirus* interactions decreased with time, there was still a large number of behavioral interactions between *P. interruptus* and *H. americanus* on day 10 in the no shelter condition. This is most clearly seen when the number of interactions on day 10 are compared with the total number of *Cancer-Panulirus* interactions. The percentage of aggression shown by *Homarus* (*Homarus* threat + *Homarus* attack) on day 10 (40%) was very similar to the total percentage of aggression (39%). Likewise, the amount of fleeing (*Panulirus* walk away + *Panulirus* abdomen flex) shown by *Panulirus* on day 10 (55%) was similar to the total percentage of fleeing (63%). Thus, although the absolute number of behavioral interactions decreased with time, the relative amounts of *Homarus* aggression and *Panulirus* fleeing remained the same as the total percentages. These data suggest that, even if the number of encounters in the field between introduced *H. americanus* and *P. interruptus* were small, the behavioral actions by *H. americanus* would be largely aggressive and the responses by *P. interruptus* defensive.

Locomotion

Homarus vs. *Panulirus* with No Shelter

The total numbers of *P. interruptus* observed roaming during the three observation periods, precontrol 1,277, experimental 1,271, and postcontrol 1,171, were not significantly different (Table 4; $P < 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks). A comparison of the three observation periods showed that the majority of this roaming by both *P. interruptus* and *H. americanus* occurred during the 1510-1700 h observation period. In *P. interruptus*, 62% of the roaming occurred during this period. In *H. americanus*, 81% of the roaming occurred during the 1510-1700 h observation period.

The relationship between the amount of time spent roaming by *H. americanus* and the number of *Homarus*-initiated behavioral actions is shown

TABLE 4.—The total number of *Panulirus interruptus* roaming during precontrol (*Homarus* absent), experimental (*Homarus* present), and postcontrol (*Homarus* absent) periods for shelter and no shelter conditions. Values for the experimental period are one-half the 10-day total so that the totals shown for the three periods are comparable. The maximum number of roaming lobsters possible for each group, during each period and for each condition (shelter or no shelter) was 2,250.

	Precontrol		Experimental		Postcontrol	
Group	Shelter	No shelter	Shelter	No shelter	Shelter	No shelter
1	27	214	97	197	30	308
2	99	361	56	252	12	125
3	168	55	132	213	106	358
4	282	89	156	207	63	62
5	129	558	125	402	154	318
Totals	705	1,277	566	1,271	365	1,171

in Table 5. There was a significant correlation ($r_s = +0.90, P = 0.05$) between the total roaming time of each *H. americanus* ($N = 5$) and the number of *Homarus*-initiated behavioral actions. That is, the greater the total roaming time, the greater was the number of behavioral actions.

TABLE 5.—Total *Homarus*-initiated behavioral actions and roaming time for shelter and no shelter conditions. *Homarus*-initiated behavioral actions include social contact, *Homarus* approach, *Homarus* threat, and *Homarus* attack. Social contact includes some *Panulirus*-initiated actions; however, the great majority of the total is due to *Homarus*-initiated actions.

	Shelter				No shelter			
Group	Sex	Size (g)	Roaming (s)	Behavioral actions	Sex	Size (g)	Roaming (s)	Behavioral actions
1	♂	419	6,435	72	♀	480	15,665	442
2	♀	469	2,785	84	♀	635	33,590	541
3	♂	457	1,650	55	♂	467	20,005	514
4	♂	471	1,735	26	♂	457	23,125	725
5	♀	430	2,025	32	♀	417	9,435	293

Homarus vs. *Panulirus* with Shelter

The numbers of *P. interruptus* roaming during the three observation periods were: precontrol 705, experimental 566, and postcontrol 365 (Table 4). The differences between the three test periods were not significant ($P > 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks).

The majority of roaming that occurred in both *P. interruptus* and *H. americanus* took place during the 1510-1700 h observation period as in the no shelter condition. Seventy-seven percent of *P. interruptus* roaming and 78% of *H. americanus* roaming occurred during this period. The amount of roaming done by *H. americanus* in the shelter condition was not significantly correlated with the number of *Homarus*-initiated behavioral actions (Table 5; $r_s = +0.60, P > 0.05$).

The amount of *P. interruptus* roaming without shelter was significantly greater than the amount of roaming with shelter (Table 4; $P = 0.028$, Mann-Whitney U test). Similarly, the amount of *H. americanus* roaming without shelter was also significantly greater than the amount of roaming with shelter (Table 5; $P = 0.004$, Mann-Whitney U test).

Panulirus vs. *Cancer* with No Shelter

The number of *P. interruptus* roaming during the three observation periods was: precontrol 532, experimental 534, and postcontrol 549 (Table 6). There were no significant differences in the amount of roaming during the three observation periods ($P > 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks).

TABLE 6.—The total number of *Panulirus interruptus* roaming and within 30 cm of the wall during the precontrol (*Cancer* absent), experimental (*Cancer* present), and postcontrol (*Cancer* absent) periods for the *Panulirus* vs. *Cancer* no shelter condition. The maximum number of roaming lobsters for each group during each period was 1,000. The maximum number of wall + no wall positions for each group during each period was also 1,000.

	Precontrol		Experimental		Postcontrol	
Group	Wall	Roaming	Wall	Roaming	Wall	Roaming
1	967	11	956	44	997	20
2	873	168	828	169	748	196
3	925	127	952	112	901	104
4	922	160	913	118	909	76
5	953	66	865	91	810	153
Totals	4,640	532	4,514	534	4,365	549

Distribution of *Panulirus*

Homarus vs. *Panulirus* with No Shelter

The displacement effect *H. americanus* had on *P. interruptus* is clearly shown in Table 7. During the precontrol observation period (*Homarus* absent) *P. interruptus* was most frequently found within 30 cm of the wall. In all five replicate experiments the subjects spent the majority of their time near the wall. Group 5 was observed within 30 cm of the wall three times more frequently than it was observed away from the wall. The other groups exhibited even greater wall—no wall differences. For example, Group 3 was

observed within 30 cm of the wall 13 times more frequently than it was observed away from the wall (Table 7).

TABLE 7.—The total number of *Panulirus interruptus* within 30 cm of the wall during the precontrol (*Homarus* absent), experimental (*Homarus* present), and postcontrol (*Homarus* absent) periods for the no shelter condition. The maximum number of positions (wall + no wall) for each group during each period was 2,250. Values for the experimental period are one-half the 10-day total so that the totals shown for the three periods are comparable.

	Precontrol		Experimental		Postcontrol	
Group	Wall	No wall	Wall	No wall	Wall	No wall
1	1,998	252	360	1,890	1,959	291
2	1,967	283	500	1,750	713	1,537
3	2,094	156	723	1,527	1,592	658
4	2,011	239	964	1,286	2,162	88
5	1,684	566	1,496	754	1,432	818

During the experimental observation period (*Homarus* present) *P. interruptus* was usually found in the center of the tank (no wall). Four of the five groups were observed more frequently in the center of the tank than within 30 cm from the wall. Only Group 5 was observed near the wall more frequently than in the center. However, Group 5 spent less time near the wall during the experimental period than in the precontrol period.

During the postcontrol period, four out of five groups were observed within 30 cm of the wall more frequently than in the center (Table 7). Group 2 spent approximately twice as much time in the center than within 30 cm of the wall.

The wall-no wall distribution of *P. interruptus* during the three observation periods was significantly different ($P = 0.009$, Kruskal-Wallis One-Way Analysis of Variance by Ranks). The sums of ranks for the three observation periods were: precontrol 59, experimental 19, and postcontrol 42. These sums of ranks indicate that the differences are between the experimental and control periods. There were no significant differences between the precontrol and postcontrol periods ($P > 0.05$, Mann-Whitney U test; Siegel, 1956).

Homarus vs. *Panulirus* with Shelter

In the shelter condition individuals of all five groups spent most of their time in the shelters (Table 8). There were no significant differences between the precontrol, experimental, and postcontrol observation periods for the number of *P. interruptus* observed in shelters ($P > 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks).

TABLE 8.—The total number of *Panulirus interruptus* in shelters or within 30 cm of the wall during the precontrol (*Homarus* absent), experimental (*Homarus* present) and postcontrol (*Homarus* absent) periods for the shelter condition. The maximum number of positions (shelter + wall + no wall) for each group during each period was 2,250. Values for the experimental period are one-half the 10-day total so that the totals shown for the three periods are comparable.

	Precontrol		Experimental		Postcontrol	
Group	Shelter	Wall	Shelter	Wall	Shelter	Wall
1	2,217	23	2,036	166	2,163	86
2	2,076	110	1,635	434	2,160	66
3	1,372	694	1,449	643	1,982	255
4	1,639	490	1,714	427	1,780	298
5	1,862	356	1,893	285	1,966	252

The wall-no wall distribution of *P. interruptus* for the three observation periods also was not significantly different (Table 8; $P > 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks). The greatest number of *P. interruptus* found outside the shelters (wall and no wall condition) occurred during the 1510-1700 h observation period.

Panulirus vs. *Cancer* with No Shelter

During the precontrol, experimental, and postcontrol periods, individuals of all five groups of *P. interruptus* were observed within 30 cm of the wall much more frequently than in positions 30 cm away from the wall (Table 6). The groups were observed near the wall from approximately 3 (Group 2 postcontrol) to 332 (Group 1, postcontrol) times more frequently than away from the wall. Group 1 spent nearly all its time near the wall during the postcontrol period. There were no significant differences in the number of lobsters found near the wall for the three periods ($P > 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks).

Discussion of Lobster Distribution and Locomotion

The effect of the presence of *H. americanus* on the distribution of *P. interruptus* in a tank without shelter is quite evident. *Homarus americanus* displaced *P. interruptus* from its preferred

areas (areas within 30 cm of the wall). There was a reversal of the precontrol wall position of four out of five *P. interruptus* groups during the experimental period (Table 7). When *H. americanus* was removed for the postcontrol period, three of the four groups which had reversed their precontrol position during the experimental period moved back to the wall position. Group 2 remained in the no wall position during the postcontrol. The exact reason for this is unknown, but perhaps this group's encounters with *H. americanus* were somehow more intense and thus the enounters had a more lasting effect on the behavior of Group 2. The individual used in this group was by far the most active *H. americanus* tested for both the shelter and no shelter condition and initiated the second highest number of behavioral actions (Table 5).

Group 5 remained in the wall position more than the no wall position during all three test periods. Thus, the *H. americanus* introduced to this group had little effect on its distribution within the tank. The reason for this is probably the low level of activity and aggression shown by this individual. It showed the least amount of roaming (approximately one-half the value shown by the next least active individual) and the lowest number of behavioral actions of any lobster in the no shelter condition. It directed only 16 attacks at *P. interruptus*, less than one-half of those shown by the next least aggressive *H. americanus*.

In contrast to the above, *C. antennarius* had no effect on the distribution of *P. interruptus* in the absence of shelter. All five groups of *P. interruptus* spent nearly all their time near the wall during each of the three test periods (Table 6). That is, *P. interruptus* groups were never observed spending more time in the no wall position than in the wall position when paired with *C. antennarius*.

Douglis (1946) found that when *H. americanus* was present in a large aquarium tank with one or more blue crab, *Callinectes sapidus*, spider crab, *Libinia emarginata*, or hermit crab, *Pagurus polycarus*, "it tended by pushing and fighting to keep the crabs on the opposite side of the tank from itself." Thus, although details were not given, it appears that *H. americanus* displaced crabs that, by virtue of their claws, would seem to be much better prepared to cope with *H. americanus* than is *P. interruptus*.

The presence of more shelter than was necessary for the number of lobsters in a tank substantially decreased the number of *P. interruptus* displaced from the wall position. This was primarily due to the fact that when shelter was present, all lobsters spent the majority of their time in the shelter. This interpretation is supported by comparing data on the roaming time for the shelter and no shelter conditions. The presence of shelter significantly reduced the amount of roaming in both *P. interruptus* and *H. americanus*.

The greater frequency of agonistic interactions observed between *H. americanus* and *P. interruptus* during the 1510-1700 h observation period, as compared with the 0800-1000 and 1200-1400 h observation periods, was also no doubt due to the higher level of locomotion during this period.

A great amount of variability in the activity and aggression of individual *H. americanus* was also observed in our study. Some individuals were very active and aggressive, while others were neither. In our study these variables were not related to the sex or size of *H. americanus*. In the shelter condition, a female exhibited the greatest number of behavioral actions, while in the no shelter condition, it was a male. Of the 10 *H. americanus* tested, these lobsters ranked fourth and seventh in size (Table 5).

CONCLUSIONS

Although we cannot predict with certainty the effect a large introduced population of *H. americanus* would have on *P. interruptus* and other decapod crustaceans native to southern California, our data suggest that an adverse outcome from such an introduction could occur. The types of behavioral interactions we observed in the laboratory between *H. americanus* and *P. interruptus* would most likely also occur in the field. This conclusion is strengthened by the studies and observations of other workers who have compared and found close agreement between the laboratory and field behavior. Our data show that a large percentage of the behavioral actions of *H. americanus* toward *P. interruptus* probably would involve aggressive actions. Assuming that individuals of these two species came in contact with one another in nature, these aggressive actions could have direct or indirect effects on the distribution and abundance of *P. interruptus*. Thus, our evidence suggests that it would

be inadvisable to introduce *H. americanus* into southern California waters.

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MERCENARIA MERCENARIA (MOLLUSCA: BIVALVIA): TEMPERATURE-TIME RELATIONSHIPS FOR SURVIVAL OF EMBRYOS AND LARVAE[1]

V. S. KENNEDY,[2] W. H. ROOSENBURG,[3] M. CASTAGNA,[4] AND J. A. MIHURSKY[3]

ABSTRACT

To estimate the effects of entrainment of *Mercenaria mercenaria* embryos and larvae in the cooling-water systems of steam-electric power plants, we used a thermal gradient apparatus. Cleavage stages, trochophore larvae and straight-hinge veliger larvae were subjected to 11 different temperatures for 8 different time periods. There was a direct relationship of mortality with temperature increase and, at higher temperatures, with increase in time exposure. As the clams aged, temperature tolerance increased, with cleavage stages most sensitive to higher temperature and straight-hinge larvae least sensitive. Multiple regression analyses of percentage mortality on temperature and time produced estimating equations that allow prediction of percentage mortality under different conditions of temperature and time exposure. Entrainment of *M. mercenaria* embryos and larvae in cooling systems of power plants should be as short as possible if mortality is to be held to a minimum.

Passage of plankton through the cooling system of steam-electric power plants is a matter of concern (Coutant, 1970). Mortality caused by such entrainment (e.g. Marcy, 1971) might lead to loss of species from the vicinity of a power plant, with various ecological and economic consequences. It is estimated that increased demand for cooling water may necessitate the location of power plants in estuarine and marine environments (Tarzwell, 1972). Thermal tolerances of planktonic organisms in these environments must be determined to allow estimation of lengths of entrainment and increases in temperature that are least harmful to entrained organisms.

The hard clam, *Mercenaria mercenaria* (L.), is an abundant and commercially important bivalve found in shallow inshore waters of the east coast of North America. It is easily spawned in the laboratory and has been the subject of numerous investigations on the influence of various factors on its larval biology (see Loosanoff and Davis, 1963; Calabrese and Davis, 1970 for appropriate references). We used an aluminum thermal gradient apparatus (Thomas, Scotten, and Bradshaw, 1963) to determine thermal tolerances of hard clam embryos and larvae at different combinations of temperature and time exposure. This simulated exposure of these organisms to heat for varying time periods in power plant cooling systems. The research was undertaken in the summer of 1972 and spring of 1973 at the Eastern Shore Laboratory, Virginia Institute of Marine Science, Wachapreague, Va. Similar experiments have been made on embryos and larvae of the coot clam, *Mulinia lateralis* (Say) (Kennedy et al., 1974). Reference should be made to that paper for fuller details of experimental apparatus and techniques.

MATERIALS AND METHODS

Mercenaria mercenaria were stimulated to spawn by fluctuating water temperatures (Loosanoff and Davis, 1963) over the range of 22° to 30°C. Gametes from 3 to 32 females and 2 to 30 males were pooled in each experiment to provide genetic diversity (Calabrese and Davis, 1970). We used three developmental stages: early cleavage stages (2 h old); trochophore larvae (10-11 h); straight-hinge veliger larvae (32-50 h).

Wild stock collected as needed in the summer near Wachapreague provided the gametes. After the experiments ended in 1972, the preservative

[1]Contribution No. 565 of the Natural Resources Institute, University of Maryland and Contribution No. 552 of the Virginia Institute of Marine Science.

[2]Natural Resources Institute, University of Maryland, Chesapeake Biological Laboratory, Solomons, Md.; present address: Fisheries Research Board of Canada, Biological Station, St. John's, Newf., Can.

[3]Natural Resources Institute, University of Maryland, Chesapeake Biological Laboratory, Solomons, MD 20688.

[4]Virginia Institute of Marine Science, Eastern Shore Laboratory, Wachapreague, VA 23480.

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TABLE 1.—Percentage mortality of cleavage stages of *Mercenaria mercenaria* under different temperature-time combinations. Values in parentheses are temperatures corrected for the influence of injection water.

Time (min)	Temperature °C										
	17.5	20.2	22.7	25.1	27.6	30.0	32.5	34.9	37.4	39.7	42.4
1	0	39	14	12	12	35	0	0	3	26	85
	(18.8)	(21.5)	(23.3)				(31.6)	(34.0)	(35.8)	(37.7)	(39.4)
5	26	0	24	11	21	0	0	12	64	99	100
	(18.4)	(21.1)	(22.7)				(31.9)	(34.3)	(36.4)	(38.5)	(40.3)
10	22	0	12	0	16	0	0	78	98	100	100
	(18.3)	(21.0)						(34.1)	(36.4)	(38.5)	(40.8)
30	0	16	1	0	8	40	63	100	100	100	100
60	11	0	12	0	22	46	88	100	100	100	100
120	0	0	10	0	16	0	91	100	100	100	100
180	0	7	0	28	0	54	72	100	100	100	100
360	21	0	0	0	0	0	98	100	100	100	100

TABLE 2.—Percentage mortality of trochophore larvae of *Mercenaria mercenaria* under different temperature-time combinations. Values in parentheses are temperatures corrected for the influence of injection water.

Time (min)	Temperature °C										
	17.6	20.1	22.6	25.0	27.5	29.9	32.4	34.8	37.3	39.7	42.3
1	29	19	14	0	0	2	11	0	0	14	20
	(18.9)	(21.4)	(23.2)				(31.5)	(33.9)	(35.7)	(37.7)	(39.3)
5	25	30	19	14	0	0	0	0	0	41	93
	(18.5)	(21.0)	(22.6)				(31.8)	(34.2)	(36.3)	(38.5)	(40.2)
10	25	21	2	3	1	0	0	0	2	86	100
	(18.4)	(21.1)						(34.1)	(36.3)	(38.5)	(40.7)
30	20	13	0	17	8	1	2	10	55	100	100
60	20	0	5	7	6	0	0	0	100	100	100
120	17	0	0	0	0	0	0	63	100	100	100
180	18	1	0	0	0	0	0	100	100	100	100
360	11	8	7	10	0	3	47	100	100	100	100

TABLE 3.—Percentage mortality of straight-hinge larvae of *Mercenaria mercenaria* under different temperature-time combinations. Values in parentheses are temperatures corrected for the influence of injection water.

Time (min)	Temperature °C										
	18.3	21.0	23.5	26.1	28.5	30.9	33.4	35.8	38.2	40.7	43.1
1	3	2	3	2	2	3	4	4	3	5	4
	(19.6)	(21.6)				(30.0)	(32.5)	(34.2)	(36.4)	(38.4)	(40.1)
5	3	3	3	5	5	4	6	4	4	4	5
	(19.2)					(30.3)	(32.8)	(34.8)	(37.0)	(39.2)	(41.0)
10	3	3	3	4	3	4	3	5	5	5	7
	(19.1)							(35.0)	(37.2)	(39.5)	(41.5)
30	3	2	3	3	4	3	5	5	8	5	29
60	5	4	2	4	4	4	5	7	5	47	76
120	3	3	5	2	5	4	5	3	9	13	99
180	5	4	4	4	6	3	3	11	6	12	96
360	4	4	4	5	5	6	4	8	9	97	98

in most of the vials containing the cleavage stages and trochophores was found to have developed a precipitate that hindered microscopic analysis of the results. Consequently, in March 1973 we spawned 2-yr-old individuals of the F_2 generation produced in the hatchery in 1971 from the same local wild stock. These clams had been held in beds near the hatchery. They were conditioned for 6 wk in warm water before being spawned (Loosanoff and Davis, 1963) and provided us with replacement cleavage stages and trochophore larvae. Results of experiments using these replacements did not appear to differ from preliminary results of the 1972 experiments.

Embryos and larvae not used immediately in experiments were held at ambient temperatures in 60-liter plastic containers at a density of about 33/ml (cleavage stages, trochophores) or about 17/ml (straight-hinge) with the seawater changed daily. Development appeared normal with no high mortalities observed. Larvae not used in our experiments were successfully carried through to metamorphosis.

We used clarified, ultraviolet irradiated seawater (28-31‰) in the experiments. The cast aluminum block, bored to hold 88 test tubes (25 mm) in an 8 + 11 matrix (see Figure 1, Kennedy et al., 1974) provided a thermal gradient

that was approximately linear, varying by 2.3° to 2.7°C from one column of test tubes to the next. Each of the 11 columns in the block represented a different temperature level (Tables 1-3). Temperatures rarely varied more than ± 0.3°C either within a test tube or from one test tube to another in a column. The eight rows represented different time exposures (1, 5, 10, 30, 60, 120, 180, 360 min). There were a total of 88 different temperature-time combinations or treatments.

Twenty-six milliliters of water placed in each test tube were brought to stable temperature levels. Four milliliters of water containing the appropriate developmental stages were injected into each test tube to give a concentration of about 9 to 12 animals/ml. We inoculated the 11 test tubes in any row simultaneously, using an apparatus holding 11 syringes whose plungers were depressed together (see Figure 1, Kennedy et al., 1974).

Eighty-eight plastic beakers, each holding about 340 ml of seawater, were placed in an 8 × 11 matrix in a water bath at 25° to 26°C. When a time period in the block ended, we removed the appropriate row of 11 test tubes at once and washed the contents of each test tube into its corresponding beaker. Survivors were incubated in the beakers for 19 h (trochophores) or 23 h (cleavage stages, straight-hinge) after the experiments ended. Preliminary experiments indicated that this allowed surviving cleavage stages and trochophores to develop to the straight-hinge stage and bacteria to decompose dead individuals. It also allowed bacteria to decompose the meat of dead straight-hinge larvae.

At the end of the incubation period, the animals in each beaker were preserved in 1% buffered Formalin.[4] Numbers of straight-hinge larvae that were alive or dead at the end of an experiment were counted for each treatment. Indications of death included an empty shell or decomposing meats within a shell. For each experiment, we used 10 control test tubes held at room temperature, with the experimental animals treated to all handling described except exposure in the block. Three experiments were made on each of the three developmental stages.

Temperature of the injected water was about 23° to 25°C. This altered the temperature in the test tubes at the cold and warm ends of the block for a short period of time after injection. We made approximate corrections for these changes (Kennedy et al., 1974), and the corrected temperatures are noted in Tables 1 to 3. No corrections were made for periods longer than 10 min.

In a separate experiment, we measured oxygen levels in the test tubes over a 6-h period using straight-hinge larvae of *M. mercenaria*. Numbers of larvae were similar to numbers used in temperature-time experiments. Over the temperature range of 18° to 43°C, dissolved oxygen levels remained near saturation, with almost no change during the 6 h. We concluded that there would be no stress from low oxygen levels (Morrison, 1971) so we did not aerate during the experiments.

Multiple regression analyses of percentage mortality on temperature and time were calculated by a UNIVAC 1108 using a BMD02R stepwise regression program, version of 2 May 1966, from the Health Sciences Computing Facility, University of California at Los Angeles.

Davis and Calabrese (1964) indicated that accuracy in experiments involving sampling and handling bivalve larvae is about ± 10%. Thus, differences of less than 20% in percentage mortality from one treatment to another may not be meaningful.

RESULTS

There was a direct relationship of mortality with temperature increase and, at higher temperatures, with increase in time exposure (Tables 1-3; Figures 1-3). As the animals aged, temperature tolerance increased, with cleavage stages most sensitive to higher temperature and straight-hinge larvae least sensitive (Tables 1-3; Figures 1-3).

The general mortality patterns for the triplicated experiments at each developmental stage were scrutinized and judged to be similar so the data were combined. Over the (approximately) 20° to 26°C interval (columns 2 to 4 in the block), survival was high at each temperature level. The average number of straight-hinge larvae found alive in each of these columns and in the controls were compared, with no significant differences found ($P > 0.05$). Therefore there was no unusual

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

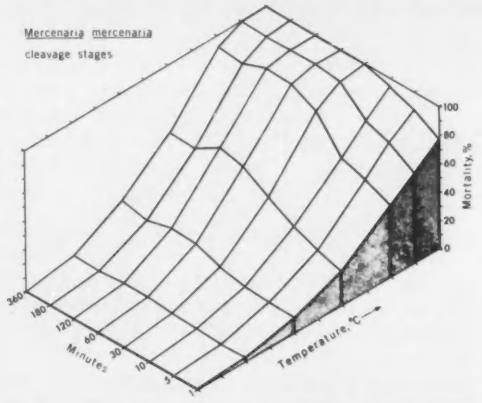

FIGURE 1.—*Mercenaria mercenaria* cleavage stages. Response surface generated from multiple regression analysis of percentage mortality on temperature and time. Refer to Table 1 for appropriate temperatures.

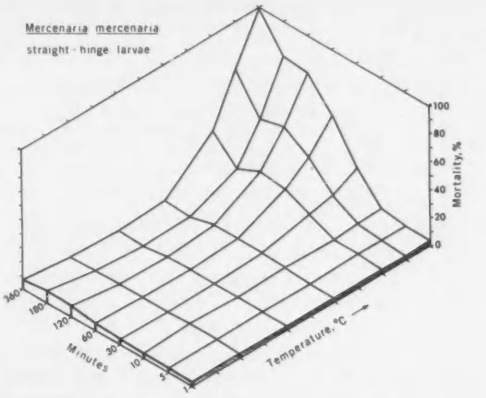

FIGURE 2.—*Mercenaria mercenaria* trochophore larvae. Response surface as in Figure 1. Refer to Table 2 for appropriate temperatures.

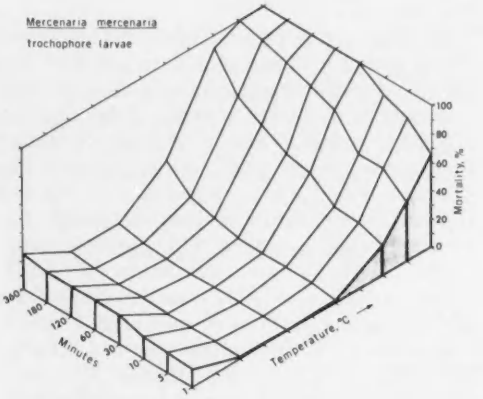

FIGURE 3.—*Mercenaria mercenaria* straight-hinge larvae. Response surface as in Figure 1. Refer to Table 3 for appropriate temperatures.

mortality associated with exposure in the block at normal temperatures (Kennedy et al., 1974). Percentage mortality data for each developmental stage were determined as for *Mulina lateralis* (Kennedy et al., 1974) and are presented in Tables 1 to 3. The stepwise multiple regression program transformed these data to arcsine square root of the percentage mortality to allow the distribution to approximate the normal. First, second, and third order terms for main effects (temperature, time) and all possible interactions were scrutinized. Only those terms (variables) with $F \geq 3.96$ ($P = 0.05, d.f.\ 1, 80$) were entered in the final equation. The program selected variables making greatest reduction in residual sum of squares until no further variables satisfied the acceptance criteria. The final empirical models appeared to be good predictive equations for all three stages (Table 4). The derived constant and variables selected for each stage are presented in Table 5, along with other statistics. The equations incorporating these constants and variables allow calculation of predicted percentage mortality for different combinations of temperature and time. The resulting estimates are in transformed form and must be converted to untransformed values (Sokal and Rohlf, 1969). Figures 1 to 3 were constructed using these equations and seven temperature levels to outline the basic pattern of the estimated response surface.

For each stage, the coefficient of determination ranged between 71% to 80% when all the variables were selected (Table 5), indicating that most of the variation in mortality can be explained by these variables (Steel and Torrie, 1960). For cleavage stages and trochophore larvae, T^3, by itself, was the best single predictor of percentage mortality. This was also true for straight-hinge larvae although T^3 was eventually eliminated by the program as new variables entered. In combination with the other variables in the final predictive equation, T^3 continued to be the most useful variable in estimating or predicting percentage mortality for trochophore larvae, as

TABLE 4.—Analysis of variance of multiple regression of percentage mortality on temperature and time for embryos and larvae of *Mercenaria mercenaria*. *** — significant at the 0.001 level; *d.f.* — degrees of freedom; *MS* — mean squares.

Source of variation	Cleavage stages		Trochophore		Straight-hinge	
	d.f.	*MS*	*d.f.*	*MS*	*d.f.*	*MS*
Regression	4	20557.780***	3	23484.304***	6	2903.295***
Residual	84	399.213	84	332.115	81	54.931

indicated by the values of the standard partial regression coefficients (Table 5). However, for cleavage stages, in the final predictive equation T^3 became relatively less important (Snedecor, 1956; Steel and Torrie, 1960).

The 88 residuals were tested for skewness (g_1) and kurtosis (g_2) (Sokal and Rohlf, 1969). Both statistics were normally distributed for cleavage stages ($g_1 = -1.02$; $g_2 = -1.78$). They were as follows for trochophore larvae: $g_1 = 2.02^*$; $g_2 = 0.90$ and for straight-hinge larvae: $g_1 = -0.12$; $g_2 = 5.92^{**}$ ($^*P = 0.05$; $^{**}P = 0.01$).

We estimated temperature levels for 10%, 50%, and 90% mortality for each period of time exposure by plotting percentage mortality from Tables 1 to 3 against log temperature on probability paper. These values (Figure 4) allow us to estimate the possible effects of temperature elevation over time on the survival of the different stages.

DISCUSSION

Early cleavage stages of molluscs appear to have a narrower range of tolerable temperatures than older stages (Pelseneer, 1901; Loosanoff, Miller, and Smith, 1951; Loosanoff and Davis, 1963; Goodwin, 1970; Kennedy et al., 1974). Results for *Mercenaria mercenaria* indicate that increased temperature tolerance occurred as early as the trochophore stage. This is in agreement with our results for *Mulinia lateralis* (Kennedy et al., 1974).

Cleavage stages of *Mercenaria mercenaria* were generally more temperature sensitive than those of *Mulinia lateralis* (Kennedy et al., 1974). Trochophore larvae of both species were generally similar in their thermal tolerances. Straight-hinge larvae of the hard clam were more temperature tolerant.

The sensitive cleavage stages of the hard clam are of primary importance in relation to the effects of entrainment and exposure to high temperature in cooling systems. If the cleavage stages are killed, obviously it does not matter that the next stages would be more temperature tolerant. The hard clam spawns during the summer throughout its geographical range (e.g. Loosanoff, 1937; Landers, 1954; Carriker, 1961; Porter, 1967; Chanley and Andrews, 1971). However, little precise information exists as to the temperature range for spawning. Carriker (1961) found that hard clams spawned between 22° and 30°C in Little Egg Harbor, N.J., with maximum frequency over the range of 24° to 26°C. This is in general agreement with the sparse

TABLE 5.—Statistics of multiple regression of percentage mortality on temperature and time. M = minutes; T = °C; b = regression coefficient; S_b = standard error of b; $100R^2$ = coefficient of determination (increases as each new variable is added); S_{rs} = standard error of the response surface (decreases as each new variable is added); b' = standard partial regression coefficient (absolute values).

Developmental stage	Constant	Variable	b	S_b	$100R^2$	S_{rs}	b'
Cleavage stages	−3.6	T^3	1.05×10^{-3}	1.40×10^{-4}	67.1	21.01	0.61
		MT^3	1.36×10^{-5}	4.90×10^{-6}	68.2	20.76	1.90
		M^2T^3	-9.24×10^{-8}	4.11×10^{-8}	69.9	20.34	4.40
		M^3T^3	1.61×10^{-10}	7.96×10^{-11}	71.3	19.98	2.74
Trochophore larvae	152.6	T^3	3.78×10^{-3}	4.40×10^{-4}	48.4	24.28	2.38
		T	−8.33	1.23	65.9	19.87	1.85
		MT^3	1.82×10^{-6}	4.40×10^{-7}	71.6	18.22	0.27
Straight-hinge larvae	8.7	MT^3	5.00×10^{-5}	5.87×10^{-6}	44.2	11.91	17.10
		MT^2	-2.48×10^{-3}	3.40×10^{-4}	61.7	9.92	21.74
		MT	3.43×10^{-2}	5.91×10^{-3}	69.7	8.88	8.20
		M^2T^3	-5.90×10^{-8}	1.10×10^{-8}	74.8	8.19	6.89
		M^3T^2	4.98×10^{-9}	1.11×10^{-9}	77.6	7.78	5.48
		M^3	-1.26×10^{-6}	4.33×10^{-7}	79.7	7.41	1.21

reports elsewhere (Nelson, 1928; Belding, 1931; Loosanoff, 1937; Porter, 1967). No temperatures have been published for spawning in Maryland or Virginia waters. We will assume conservatively that the range of 23° to 29°C would apply in these waters and that hard clam embryos and larvae would be present in the plankton under these conditions. Coutant (1970) estimated that the average temperature increase expected in cooling water carrying entrained organisms through a nuclear power plant would be 10.8°C. Therefore, entrained embryos and larvae of hard clams could be subjected to temperatures of 33.8° to 39.8°C while passing through such a facility. In spring (Figure 4), 90% of the cleavage stages could be eliminated if entrained for about 30 min. Fifty percent could be killed in about 13 min and 10% in about 6 min. For trochophores, 10% could be killed in about 25 min, perhaps longer. Straight-hinge larvae would appear to be unaffected by the temperature increase in spring. In late summer, 90% of the cleavage stages might be killed in 1 min or less, with 90% of the trochophores dying in less than 5 min. Over 180 min of exposure would be needed to kill 90% of the straight-hinge larvae.

The equations we have developed should allow predictive evaluations to be made concerning the effects of entrainment of hard clam embryos and larvae in Maryland and Virginia waters and elsewhere. Discharge canals of steam-electric power plants are usually located to avoid directing heated water over beds of commercial bivalves. It appears that it is also important to avoid taking in water that might come from the area of a bed of hard clams during spawning season. Should such water contain embryos and larvae of hard clams, long exposures in the cooling system of the plant (whether within the facility or in a discharge canal) could be lethal to the entrained

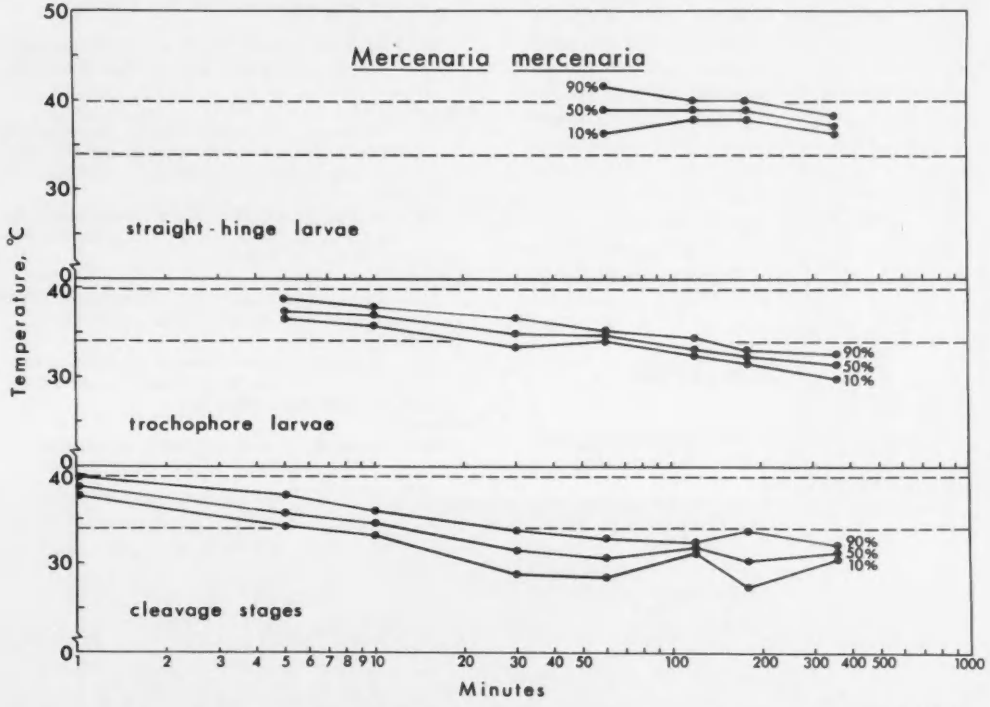

FIGURE 4.—Estimates of three percentage mortality levels for different exposure times. Percentage mortality for trochophore larvae and straight-hinge larvae was estimated to be less than 10% at 1 min and up to 30 min, respectively. For each stage, the dashed lines represent an increment of 10.8°C over estimated spawning temperature in spring (23°C - lower dashed line) and late summer (29°C - upper dashed line) in Maryland and Virginia waters.

organisms. Whether such mortality would affect the continued existence of the local hard clam resource depends upon local circumstances. Minimum destruction of the resource during use of cooling water from the vicinity of hard clam habitat requires that entrainment of embryos and larvae be as short as possible. The thermal discharge should be mixed with receiving water as quickly as possible to provide a rapid return to ambient temperature. In making evaluations it should be remembered that organisms passing through cooling systems are also subject to various stresses due to pressure changes, mechanical effects, and chlorination, in addition to temperature.

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